CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 19

UNIVERSITY OF MICHIGAN HERBARIUM
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12 MAY 1993

William Randolph Taylor

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DEDICATION

An integral part of the distinguished professional career of William Randolph Taylor was his association with the University of Michigan Herbarium, an association that spanned six decades, from the time of his arrival at the University of Michigan in 1930 to accept a professorship until the time of his death in November, 1990, at the age of 94. In addition to being a Professor of Botany, he served as Curator of Algae until his retirement and subsequently as Curator Emeritus of Algae. His remarkably long professional career was highlighted by many accomplishments that brought him a national and international reputation of the highest rank and added considerable luster to the University of Michigan Herbarium.

Randolph Taylor was a keen microscopist at an early age and had an abiding fascination with natural history. A native of Philadelphia [I found it amusing that he always regarded himself as "a Philadelphian" even after living in Ann Arbor for more than 60 years], he received his entire education in the Philadelphia area, earning his B.S. (1916), M.S. (1917), and Ph.D. degree in botany (1920) from the University of Pennsylvania. He became a faculty member at the same institution and was named a professor of botany in 1927. Reflecting initially broad interests in cytology and plant anatomy, his first publication, treating the artificial induction of cambia, appeared in 1919. He carried out cytological studies on maple (*Acer*) and later turned his attention to several monocotyledonous genera. Gradually his research interests focused on algae, both freshwater and marine forms. He was involved in field work in the mid-1920's in such disparate sites as the remote Selkirk Mountains of eastern British Columbia and the Dry Tortugas in the Gulf of Mexico. A lengthy paper on the alpine algal vegetation of the mountains of British Columbia appeared in 1928, during the same year that he authored a book-length treatment of *The Marine Algae of Florida, with special reference to the Dry Tortugas*.

Early on Dr. Taylor appreciated the need to catalog plant diversity, particularly that of the seas. He was invited to participate in expeditions sponsored by Allan Hancock to the Caribbean, Pacific Mexico, and Central and South America, including the Galapagos Islands. Books published in 1942 and 1945 summarize these research efforts. Then in 1946 he served as a senior biologist in "Operation Crossroads" of the Department of Navy, which allowed him to conduct a botanical survey of Bikini and other Marshall Islands in the South Pacific prior to and immediately after the testing of atomic bombs. His book *Plants of Bikini and other Northern Marshall Islands* (1950) was the fruit of these labors. Over the years, in light of his growing reputation as an authority on the systematics of the algae, he was the recipient of the collections made by assorted scientific expeditions, notably those of the US ships *Hassler* (1871–72) and *Albatross* (1887–88), to Brazil and southern South America. Similarly, he worked up collections made by the 1937 Smithsonian-Hartford Expedition to the West Indies, the 1960 Smithsonian-Bredin Expedition to Yucatan and their 1957 Expedition to the Society and Tuamotu islands. Earlier, he had published on the freshwater flora of Newfoundland, which resulted from his being entrusted with the collections made by a Harvard-Pennsylvania expedition to that province.

It is clear that certain tropical genera, often widely distributed ones with many species, appealed to Dr. Taylor as worthy of particular scrutiny. Examples include the brown algal genera *Turbinaria* and *Sargassum*, the red algal genera *Pterocladia* and *Gelidium*, and green algal genera *Caulerpa*, *Halimeda*, *Bryopsis*, and *Trichosolen*. His expertise in microtechnique is exemplified by his studies of post-fertilization events in the tropical red algal genera *Acrosymphyton* and *Dudresnaya*.

In 1917 Taylor was a student in a course at the Marine Biological Laboratory in Woods Hole, Massachusetts, which led to a life-long association with that institution as well as a deep commitment to the marine flora of the region. He taught a course on the algae at the M. B. L. for many summers. He was a Lifetime Trustee of the M. B. L. and also a Life Trustee of the Bermuda Biological Station. It was at the Marine Biological Laboratory that he met Jean Falconer Grant from Virginia, a student in his course, whom he married in 1926. For almost 64 years Jean Taylor was a steadfast and selfless companion assisting Randolph in his scientific pursuits in the field, at the University, and at Woods Hole. He recognized Jean's making it all possible for him by dedicating his books to her with the words "in appreciation for the patience and encouragement." Dr. Taylor is survived by Jean and their sons William R., Jr., and James Keith as well as three grandchildren, W. R. Taylor III, Carol Ann Taylor, and Patricia Jean Taylor.

Undoubtedly, Dr. Taylor's lasting mark is derived from his major floristic treatments *Marine Algae of the Northeastern Coast of North America* (1937 and the revised edition in 1957) and *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas* (1960). If one happens to be visiting marine labs as far north as Newfoundland or southward to southern Brazil, one finds that his two floristic treatments continue to serve as the basic sources of information for marine botanists. These monumental efforts represent a synthesis of many years of arduous field work and painstaking laboratory work, supplemented by careful examination of types and other reference collections in various herbaria in Europe and North America. He was very cognizant of the need to check out the old and often obscure literature. He kept fastidious records of his observations from his own field work and his perusal of specimens on his travels to herbaria in London, Paris, Lund, Copenhagen, and Uppsala. For the next generation of researchers he left behind his notebooks dating back to 1921 as well as a holograph and autograph collection of hundreds of botanists with whom he carried out correspondence. During such a long career he had the good fortune of corresponding with such eminent phycologists as Howe, Kylin, Fritsch, Hamel, Pascher, Yamada, Setchell, Skottsberg, Børgesen, Feldmann, and many others.

Another important aspect of Dr. Taylor's legacy lies in the students that he had trained. These include both phycologists and cytologists who received their doctoral degrees under his tutelage: H. T. Croasdale, C. K. Tseng, C.-C. Jao, R. C.-Y. Chou, E. M. Hulburt, W. J. Gilbert, J. L. Blum, S.-H. Wu, F. Thivy, R. T. Wilce, L. Hillis-Colinvaux, W. Adey, and A. J. Bernatowicz. The late A. B. Joly from Brazil was a "post-doc" under Taylor and influenced a whole generation of Brazilian botanists.

Rememberances of Randolph Taylor have been published by his former students, friends, and colleagues around the world. Such tributes have appeared in *Phycologia* (30: 378–380), *British Phycological Journal* (27: 1–2), *Botanica Marina* (34: 63–67), *Taxon* (40: 350–351), *Cryptogamie: Algologique* (12: 83–85), *Japanese Journal of Phycology* (39: 77–78), *Boletim Ficológico, Sociedade Brasileira de*

Ficológia (11, No. 1: 20), and the *Phycological Newsletter* of the Phycological Society of America (27, No. 1: 7–8). His algal references, which total 122 publications, are provided in the obituary published in *Botanica Marina*.

Over the years Dr. Taylor was a frequent contributor to this series of the Michigan Herbarium, exemplified by his 1969 publication "Notes on the distribution of West Indian marine algae particularly in the Lesser Antilles." In the Introduction to that paper he conveys something of the adventure of his and Jean's "island-hopping" throughout the Caribbean. He speaks of the demanding routine of locating detailed official land maps in obscure government offices, of making local contacts that developed into information centers, of processing and drying the algal specimens, of coping with complex local postal regulations and with clerks who were often suspicious of scientific shipments, of Jean's driving rental cars over all but the most dangerous roads, and of her coaxing native dishes from cooks who considered them too much trouble. One senses the same excitement and challenge that the Taylors experienced on their Caribbean sojourns. Dr. Taylor's last paper to appear in the *Contributions* was his "Notes on marine algae from the tropical Atlantic Ocean—VIII" in 1980. Well into his retirement he remained an active figure in our ranks, the personification of scholarship and achievement. It is with a continuing sense of deep admiration and appreciation that we his Herbarium colleagues dedicate this volume of the *Contributions* to the memory of Wm. Randolph Taylor.

Michael J. Wynne

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BENTHIC MARINE ALGAE FROM THE MALDIVES, INDIAN OCEAN, COLLECTED DURING THE R/V *TE VEGA* EXPEDITION

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INTRODUCTION

The benthic marine algal flora of the Maldive Islands in the central Indian Ocean, based on a handful of sporadic accounts, is relatively poorly known. Early collections were made by the J. S. Gardiner Expedition of 1899–1900 (Gardiner 1903) and resulted in Foslie's (1903) record of 9 species of Corallinaceae and Barton's (1903) record of 6 species of green and brown algae. As a result of the Percy Sladen Trust Expedition to the Indian Ocean in 1905, also under the leadership of Gardiner (1907/1909), Gepp and Gepp (1908) reported on some Chlorophyceae and Rhodophyceae, and Weber-van Bosse (1914) listed a number of Rhodophyceae. Collecting sites of this expedition, also called the 'Sealark' Expedition, included Diego Garcia in the Chagos Archipelago, lying just to the south of the Maldives, and Cargados Carajos, lying north of Mauritius. Newton's (1953) sole report of *Microdictyon pseudohapteron* A. & E. S. Gepp f. *luciparense* Setchell (Setchell 1929) from the Maldives was based on a collection made by the John Murray Expedition of 1933–34. Tsuda and Newhouse (1966) provided the most detailed list of species from this atoll group. On the basis of collections made by Mr. David C. Sigee, they listed 27 taxa of marine Chlorophyta, 8 Phaeophyta, and 25 Rhodophyta. A number of these taxa, however, were identified only to the generic level, such as four unnamed species of *Hypnea*. Also from the Sigee collections, Hollenberg (1968a) reported the occurrence of *Polysiphonia scopulorum* Harv. var. *villum* (J. Ag.) Hollenberg and *P. upolensis* (Grunow) Hollenberg. H. E. Hacket made extensive collections at nine atolls in the Maldives on an earlier leg of the R/V *Te Vega* Expedition across the Indian Ocean, and from these Hackett collections Hollenberg (1968b) listed nine species of *Herposiphonia*. Hackett (1969) himself reported some preliminary observations, and a follow-up study by Aregood and Hackett (1971) resulted in the description of *Dictyurus maldiviensis*, a new species of Dasyaceae. Titlyanov and Butorin (1978) published a short list of the algae collected from two atolls of the Maldive Islands. For this region of the Indian Ocean, Srinivasan's (1960) account is pertinent, since he discussed distribution patterns of benthic marine algae for the east and west coasts of India as well as for the archipelagos of the Lakshadweep Islands (formerly the Laccadives) and Mimicoy in the Arabian Sea and the Andaman and the Nicobars in the Bay of Bengal. The publications by Jagtap (1985, 1987, 1992) on the Andamans, Nicobars, and Lakshadweep Islands are also pertinent.

In late 1964, the author had the opportunity to participate in Cruise No. 5 of Stanford University's R/V *Te Vega* Expeditions, which was a series of oceano-

graphic studies supported in part by the U. S. National Science Foundation (Grant No. G17465, Dr. Donald P. Abbott, Chief Scientist). Benthic algae were collected mostly by snorkeling in shallow-water habitats in the vicinity of Mále Atoll (4.00° N, 73.28° E). A few collections were made at depths of 5–10 m by SCUBA-diving colleagues. Collection sites and supplemental data are given in the Appendix.

Collections were either preserved in 5% formalin-seawater or processed as dried herbarium specimens. Much of the material was small, turflike growths on corals. Specimens were later sorted out and mounted onto glass microscope slides, on which they were routinely stained with a mixture of 1% aniline blue/1 M HCl/ corn syrup/tap water (4:1:20:75) and allowed to solidify. Collections cited in this report have been deposited in the University of Michigan Herbarium (MICH).

LIST OF TAXA

Rhodophyta

Bangiales

Bangiaceae

Bangia halymeniae Wynne, sp. nov. Figs. 1–3.

Fila simplicia, uniseriata, crescentia diffusa cum cellulis singulis elongatis basalibus contractis in hostam (*Halymenia venusta*) affixis; fila usque ad 1.5–1.8 mm longa attingentes; cellulae vegetativae una chromatophora stellata continentes; cellulae 8–12 μm latis et 6–14 μm longis cum vaginis distinctis mucilaginis, fila uniseriata in stato vegetativo remanentia; distales partes filorum reproductivescentes, cellulis divisiones successivae subeuntibus, cellularum parvarum (apparenter spermatia) aggregatas efferentibus, 1–2 μm in diametro, 8–16 ab cellulae originale vegetativa; alia reproductio ignota.

Holotype: *Wynne 4B-25*, in MICH; type locality: Funidu Island, north of Male, Maldives. 5.xi.1964. Isotypes deposited in DUKE, L, MEL, UC, and US.

This red alga consists of unbranched, uniseriate filaments (Fig. 1d) with diffuse growth and with single elongate, tapering basal cells (Figs. 1d–f, 2), which attach the alga to its host (*Halymenia venusta*). Filaments reach lengths of 1.5–1.8 mm. Vegetative cells contain a single stellate chloroplast (Fig. 1g), which is typical of the Bangiales. Cells are 8–12 μm in breadth and 6–14 μm in length with a distinct mucilaginous sheath. Filaments remain uniseriate in the vegetative condition. Distal portions of filaments become reproductive (Fig. 3) with cells undergoing successive divisions to produce packets of small cells (presumably spermatia), 1–2 μm in diameter, and numbering 8–16 per original vegetative cell (Fig. 1a–c). This was the only method of reproduction observed.

This small alga gives the initial impression of being a species of *Erythrotrichia*, such as *E. carnea* (Dillwyn) J. Agardh (Kornmann & Sahling 1977) and *E. biseriata* Tanaka (Tanaka 1944). However, it cannot be assigned to the Compsopogonales, the order that includes *Erythrotrichia*, because of the pattern of spore production. As Drew (1956) demonstrated, "Type 1" spore formation, in which monospores are produced from differentiated sporangia (that is, by an unequal cell division which separates off the monospore by means of an arching, oblique wall) is characteristic of *Erythrotrichia* and other members of what is now known as the Compsopogonales (Bold & Wynne 1985). Drew's "Type 3" spore formation, however, in which a number of spores are produced by successive divisions

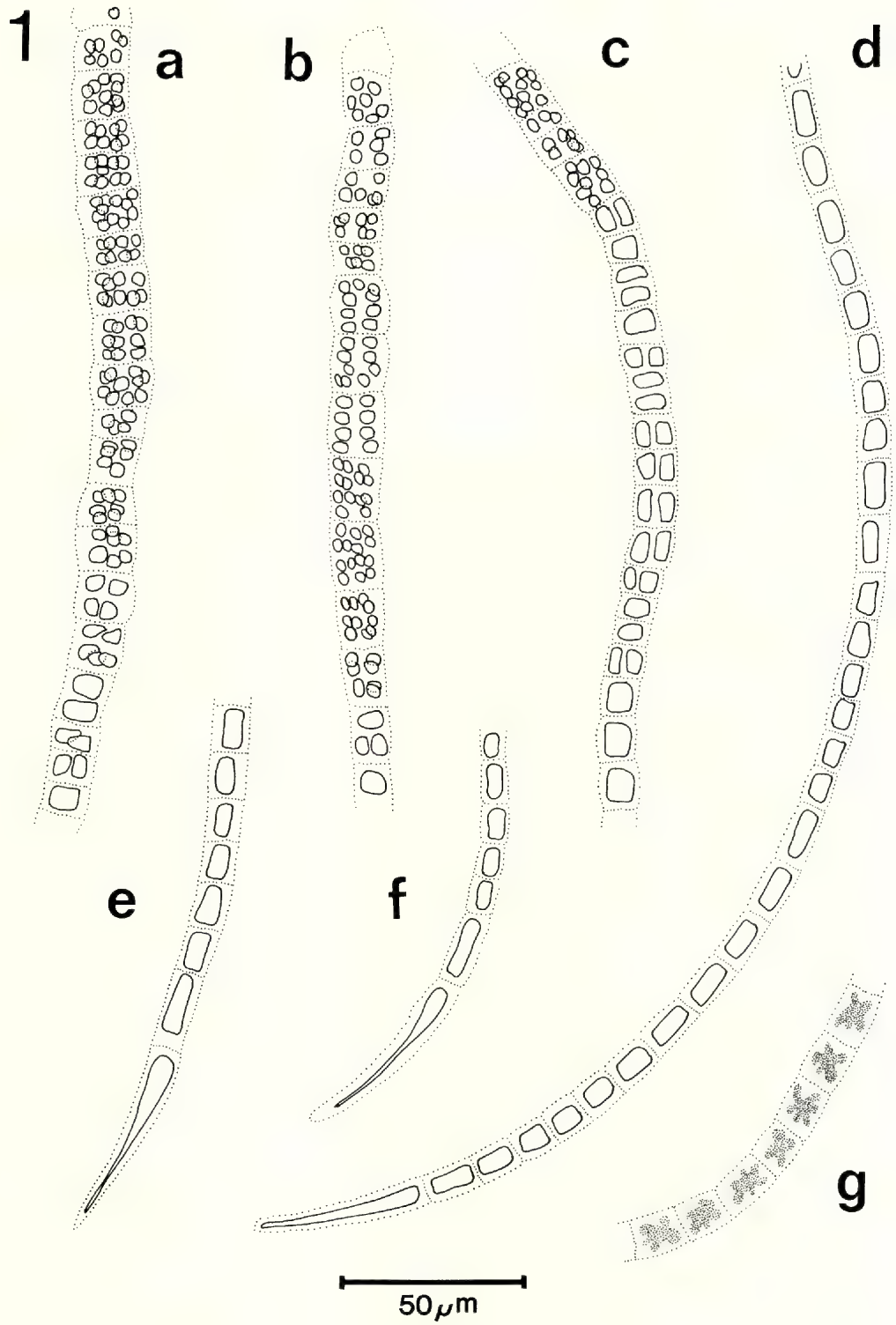
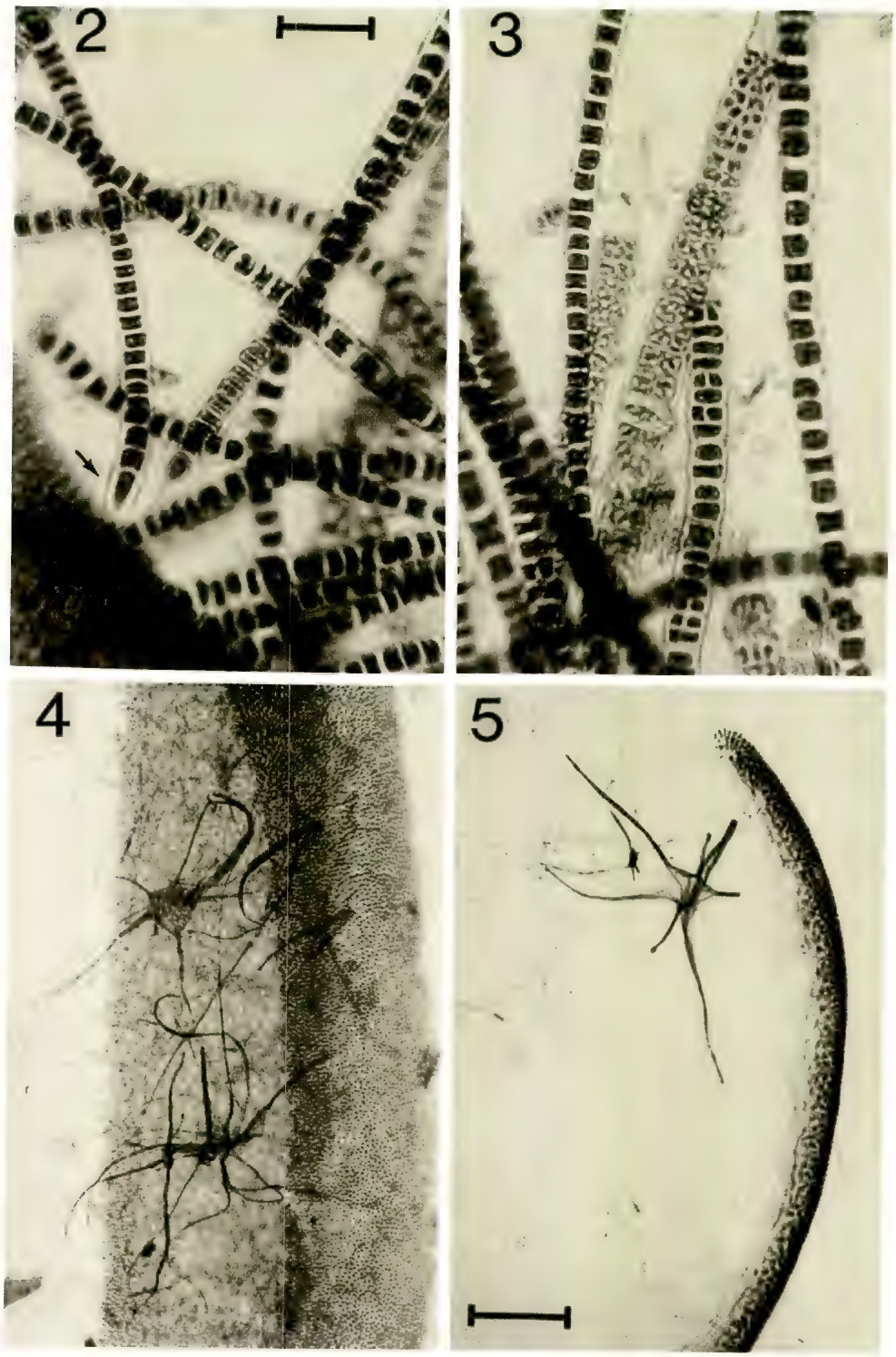


FIG. 1. *Bangia halymeniae*. a–c, reproductive distal portions of filaments; d–f, basal portions of filaments; g, portion of filament with vegetative cells, each containing a stellate chloroplast.



FIGS. 2–5. Figs. 2 , 3. *Bangia halymeniae*. Fig. 2. Thalli attached to host with elongate basal cell (arrow). Fig. 3. Reproductive thalli. Figs. 4 , 5. *Halymenia jelinekii*. Transections of blades, showing large stellate cells in medulla. Scale: bar = 50 μm in figs. 2, 3; bar = 200 μm in figs. 4, 5.

of a mother-cell, is characteristic of *Bangia* and *Porphyra*, representing the Bangiales. Clearly, this new species belongs to the Bangiales rather than the Compsopogonales (including the Erythropeltidales of Garbary et al. 1980).

The genus *Bangia* is known primarily by the widespread *B. atropurpurea* (Roth) C. Agardh. This species is now generally accepted to be broadly euryhaline, thus including *B. fuscopurpurea* (Geesink 1973; Reed 1980; Sheath & Cole 1984). Plants of *B. atropurpurea* develop from the uniseriate to the multiseriate vegetative condition and are attached by numerous rhizoidal cells at the base. So the new species is easily distinguished from the best known representative of the genus.

A number of other species of *Bangia* have been described over the years. Some of these early-described species (e.g., see Kützing 1843, 1853) remain poorly known and of uncertain status. Most species of *Bangia* become multiseriate prior to reproduction, such as *B. gloiopeltidicola* Tanaka (Tanaka 1950, 1952) and *B. enteromorphoides* Dawson (Dawson 1952), and thus are easily separable from the new species. Yet, others remain uniseriate in the vegetative condition similar to *B. halymeniae*. An example is *B. yamadai* Tanaka, but it has a basal attachment formed by rhizoids from many cells (Tanaka 1944, 1952).

Garbary et al. (1981, Fig. 9P) depicted an alga identified as *Bangia tenuis* Collins ex Gardner with a similar vegetative organization to that of *B. halymeniae*, viz., a simple uniseriate filament attached by a single elongate tapering cell. That alga is known only from the original collection made from a pool in a salt marsh on Orcas Island, Washington, and distributed as Phycotheca Boreali-Americana no. 1341; it was sterile. In addition, *B. tenuis* Gardner (1927) appears to be predated by *B. tenuis* Kützing (1843, 1849).

Bonnemaisoniales

Bonnemaisoniaceae

Asparagopsis taxiformis (Delile) Trevisan.

Collection: 4C-4 (♂).

The heteromorphic sporophytic stage of this alga, which had been reported under the name *Falkenbergia hillebrandii* (Bornet) Falkenberg (Chihara 1961), was also present.

Gelidiales

Gelidiellaceae

Gelidiella acerosa (Forsskål) Feldmann & Hamel.

Collections: 4B-2 (⊕); 4E-4.

Gelidiaceae

Gelidium pusillum (Stackhouse) LeJolis var. **pusillum.**

Collection: 4B-10 (⊕).

This small, mat-forming alga fits the description of *Gelidium pusillum* var. *pusillum* based on the key and description given by Hatta & Prud'homme van

Reine (1991). Creeping axes, firmly attached to coral substratum by multicellular peglike holdfasts, give rise to erect axes that reach only 1–4 mm in height. Erect axes are flat and simple or sparingly branched. Tetrasporangia are densely produced in sori that cover the upper surfaces of the erect blades, leaving the margins sterile.

Gigartinales

Halymeniaceae

Halymenia jelinekii Grunow. Figs. 4, 5.

Collection: 4F-1.

The anatomy of these blades, which includes large, prominent stellate cells in the inner cortex, indicate that this material belongs to *Halymenia* (Balakrishnan 1961; Abbott 1967; Codomier 1974). The identification to species is made on the basis of the relatively small size of the blades (2.5–3.0 cm in width and approximately 2.0 cm tall) and their strong resemblance to Grunow's (1867, pl. IX, fig. 2a) illustration of *H. jelinekii*. John Lewis of the University of Melbourne has concurred with this determination. Grunow depicted the blade of *H. jelinekii* as being 3.5–4.5 cm in diameter and having a short stipe (5–6 mm long) and a lobed margin densely beset with small proliferations, as in the Maldivian specimens. The blades have a transversely elliptical shape, that is, broader than tall. They are somewhat lobed but not deeply divided and are attached by a short stipe. The most distinctive feature is the densely fimbriate upper blade margin, the fimbriae being re-branched and overlapping one another.

This species was described from the Nicobar Islands and until now has been known only from the Andaman and Nicobar Islands (Krishnamurthy & Joshi 1970; Desikachary et al. 1990). Grunow compared his species to *Halymenia dubia* Bory. Certain other species of *Halymenia* share with *H. jelinekii* a similar habit of a lobed or shallowly divided blade with densely fimbriate margins. An example is *H. rotunda* Okamura (1936), which was depicted earlier by Okamura (1930, pl. 266, fig. 4–12, as "*Erythrymenia obovata*"). Another, *H. dilatata*, was described by Zanardini (1851) from the Red Sea and later depicted as a rather large, lanceolate blade, maculate, with marginal processes (Zanardini 1858, pl. V, fig. 1). Its distribution was later broadened to include Somalia, Malaysia, Japan, India, Vietnam, and South Africa (J. Agardh 1892; Okamura 1921; Weber-van Bosse 1921; Børgesen 1938; Dawson 1954a; Norris & Aken 1985). Blades of *H. dilatata* reach a length of 20–30 cm (Okamura 1921; Balakrishnan 1961). The significantly larger blade size and their maculate appearance of *H. dilatata* preclude identification of the Maldivian specimens with that species. Likewise, *H. maculata* J. Agardh, with Mauritius as type locality (J. Agardh 1885), is a larger plant, about 25 cm high (Børgesen 1950), with coarse, irregular lobes bearing fimbriate proliferations.

Some species of *Halymenia* have specific names that suggest a relationship with the Maldivian specimens of this genus. Zanardini (1874) described *H. fimbriata* and *H. multifida* from Lord Howe Island in the Tasman Sea; but these taxa have not yet been depicted in the literature and remain poorly known.

Halymenia venusta Børgesen.

Collections: 4A-1; 4B-4 (⊕).

Hypneaceae

Hypnea pannosa J. Agardh.

Collection: 4B-15 (♀, ⊕); growing on coral and epiphytic on *Halimeda taenicola.*

Features which support identification of this material as *Hypnea pannosa* include the following: a habit of a clump of much-branched, intricately organized, non-percurrent, subterete axes; ramification at close intervals, irregularly alternate; apices divaricate or obliquely truncate; tetrasporangial sori formed on one side of the branchlets (rather than encircling them as in *H. musciformis* var. *esperi*); and the presence of lenticular thickenings in the walls of medullary cells. Axes are 0.4–0.5 mm in diameter, which is at the low end of the 0.4–1.5 mm range reported for this species by Cribb (1983). Trono and Ganzon-Fortes (1980) reported main axes to be 0.3–1.7 mm broad. Final branchlets tend to be spinose.

The taxonomic opinion that *Hypnea nidulans* Setchell is conspecific with *H. pannosa* was first expressed by Dawson (1961) and later accepted by others, e.g., Cribb (1983) and Yoshida et al. (1990). Compactly intricate cushionlike mats characterize *Hypnea pannosa*. This species has a wide pantropical distribution including the Indian Ocean and the tropical Pacific Ocean. Its occurrence at Chagos Archipelago and the presence of lenticular thickenings were referred to by Tanaka (1941, as *H. nidulans*). Living thalli produce a blue-green iridescence. Axes are somewhat compressed, and apices are divaricate or obliquely truncate (Tanaka & Pham-Hoàng 1962). Tetrasporangial sori are formed as a swelling on only one side of a branch in its mid-region. This species is known to have a pantropical distribution (Weber-van Bosse 1928; Tanaka 1941; Børgesen 1943; Taylor 1960; Jaasund 1976; Mshigeni 1978; Trono & Ganzon-Fortes 1980; Cribb 1983).

Hypnea spinella (C. Agardh) Kützing.

Collection: 4B-11 (⊕).

This sprawling, mat-forming alga produces numerous attachment pads to its hosts at scattered sites along its sprawling axes. The final order of branches are usually small and spinose. The tetrasporangial sori encircle these ultimate branches. This species bears some resemblance to the co-occurring *Hypnea pannosa* [see above] but is separable both by the different position of the tetrasporangial sorus and the non-compressed, narrow axes.

The taxonomic opinion expressed by Mshigeni (1978) and Price and Scott (1993) is followed here in regarding a number of reports of *Hypnea esperi* Bory (e.g., those by Børgesen 1924; Tanaka 1941; Dawson 1954a 1957; Egerod 1971) as assignable to *H. spinella*. Dawson (1961) has traced this confusion back to Kützing's (1868) depiction of *H. esperi*, which appears to conform to *H. cervicornis* J. Agardh. Genuine *H. esperi*, which is an illegitimate name according to Silva et al. (1987), has been relegated by J. Agardh (1852) to taxonomic synonymy within *H. musciformis* (Wulfen) Lamouroux.

Some authors, such as Tanaka and Pham-Hoàng (1962) and Cordero (1977), placed *Hypnea spinella* in the synonymy of *H. cervicornis*. If these two taxa are to be regarded as conspecific, however, *H. spinella* has priority (Wynne 1986). These two species seem to be separable on the basis that in *H. spinella* the final branchlets are acute and needlelike and the axes are more prostrate, anastomosing, becoming

attached to one another and to the host by discoid holdfasts, whereas in *H. cervicornis* the final branchlets are broader and the axes are more erect, entangled but not becoming mutually attached (Lawson & John 1987; Price & Scott 1993).

Rhodymeniales

Rhodymeniaceae

Gelidiopsis intricata (C. Agardh) Vickers.

Collections: 4E-5; 4G-1.

This genus was recently transferred by Price and Kraft (1991) from the Gracilariaceae (Gigartinales or Gracilariales) to this family in the Rhodymeniales on the basis of procarp structure, early gonimoblast and fusion cell development, mature cystocarp structure, and the cruciately divided tetrasporangia. Also, Price and Kraft (1991) retained *Gelidiopsis* as a genus distinct from *Ceratodictyon* contrary to the viewpoint expressed by Norris (1987).

Champiaceae

Lomentaria mauritiana Børgesen.

Collections: 4B-24 (♀); 4C-13; 4F-11.

Axes of *Lomentaria mauritiana* have multiple attachments to the substratum and to other axes because of the random production of rhizoidal tufts. This observation is in agreement with the original account (Børgesen 1944) and a report of this taxon from the Seychelles (Wynne, submitted-A). In surface view, the outer cortical layer shows a mixture of larger cells surrounded by much smaller cells. Gland cells are borne laterally from the longitudinally running medullary cells, which are at the periphery of the hollow interior. Cystocarps were present, pericarps measuring 545–600 μm in diameter.

Ceramiales

Ceramiaceae

Centroceras apiculatum Yamada. Fig. 6.

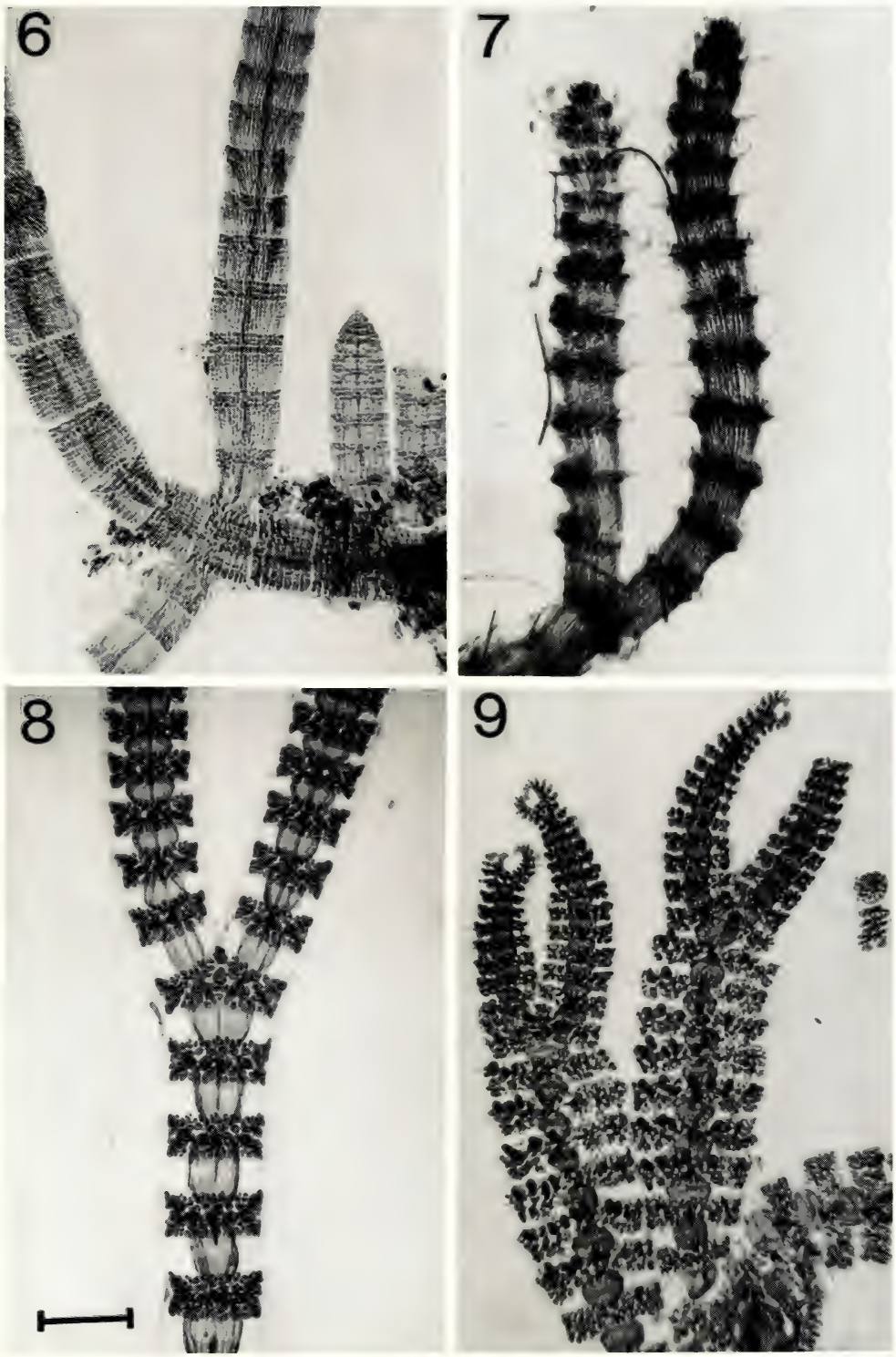
Collection: 4C-7 (⊕); 4E-17.

Described from the Atoll of Ant in Micronesia by Yamada (1944b), this species has been depicted by Dawson (1956) and Egerod (1971) on the basis of material from the Southern Marshall Islands and Thailand, respectively. Ardré (1987) observed that the periaxial cells of *C. apiculatum* each produce two ascending filaments and four descending filaments. Tetrasporangia are produced in a whorled arrangement, with 5–6 sporangia per segment, and are sunken beneath the continuous cortication, unlike the exserted position of tetrasporangia in *C. clavulatum* (C. Ag.) Mont. and *C. minutum* Yamada.

Centroceras minutum Yamada. Fig. 7.

Collections: 4C-11 (⊕).

Making use of collections originating both from the tropical Atlantic and Pacific Ocean, Ardré (1987) made comparative morphological studies of several species of *Centroceras*. She expressed the taxonomic opinion that *C. minutum*



FIGS. 6–9. Fig 6. *Centroceras apiculatum*. Vegetative thallus. Fig. 7. *Centroceras minutum*. Tetrasporangiate thallus. Figs. 8, 9. *Ceramium marshallense*. Fig. 8. Vegatative thallus. Fig. 9. Tetrasporangiate thallus. Scale: bar = 300 μm.

seems to be only a morphological variation of *C. clavulatum* (C. Ag.) Mont. It is true that the axes of both taxa have colorless multicellular spines arising at the nodes. Examining collections from the Seychelles, however, Wynne (submitted-B) chose to recognize *C. minutum* as distinct from *C. clavulatum*. He offered the following as distinguishing features: the small stature (1 cm or less in height) and narrow thickness of the internodes (only 120–130 μm thick) of *C. minutum*, the non-forcipate apices, and the sprawling, closely adherent nature of the axes due to abundant production of rhizoids. Yamada (1944b) described the cortical cells to be arranged in longitudinal but not in transverse rows. Also, *C. minutum* lacks a dichotomous habit, as pointed out by Dawson (1956).

Ceramium flaccidum (Kützing) Ardissone.

Collection: 4H-4 (⊕).

The bands of nodal cortication in this species are divided by a transverse line, and the proximal portion of the nodal band is comprised of transversely elongated cells. Tetrasporangia are produced in whorls and covered by an involucre. Gland cells are also present in the distal portions of the nodal bands. Dawson (1956), who treated this taxon under the illegitimate name *C. gracillimum* var. *byssoideum*, noted transitional forms with *C. masonii* Dawson and suspected that "only a single, widespread, variable species is involved." This concept of this large complex was further elucidated by Womersley (1978), when he regarded *C. masonii*, *C. taylorii* Dawson, *C. byssoideum* Harvey, and *C. gracillimum* Harvey as taxonomic synonyms of *C. flaccidum*.

Ceramium marshallense Dawson. Figs. 8, 9.

Collection: 4D-6 (⊕).

This alga has creeping axes, which give rise to erect axes that are dichotomously branched to several orders. Apices are strongly forcipate, and rhizoids arise from the nodes of prostrate axes. Mature axes are 90–100 (–120) μm in diameter. Eight periaxial cells are produced per node, and they cut off cortication in both directions, resulting in irregularly arranged cells lying in about 6–7 horizontal rows, with the periaxial cells still evident. The nodal cortication is discrete, with entire margins on both proximal and distal edges (Fig. 8). In young vegetative axes, nodes and internodes are approximately both as broad as deep; in older vegetative axes the internodal distances are several times that of the nodal distances. In tetrasporangiate axes, internodal distance is greatly shortened but still present. Tetrasporangia are borne at the nodes in whorls (of up to 8) and are sunken within the cortication (Fig. 9). Tetrasporangia are elongate-ovoid, measuring 25–32 × 14–20 μm and are cruciately divided.

Ceramium marshallense conforms to J. Agardh's (1894) Series 3, Periclinia of *Ceramium*, in that it bears its tetrasporangia in whorls at the nodes in the last few dichotomies of the alga. This species bears some similarity to *C. vagans* Silva [= *C. vagabunde* Daws., nom. illeg.], in which tetrasporangia are also cruciately divided and borne in whorls. However, as depicted by Dawson (1954b, pl. 4, fig. 2, as *Ceramium* sp.; 1957, fig. 27e, as *C. vagabunde*), thalli in the latter species have blunt, non-forcipate apices, differing from the circinnately inrolled apices of *C. marshallense*, lack dichotomous branching; the whorled tetrasporangia are larger in size (40 μm long), protrude from the cortical bands more noticeably, and are protected by prominently swollen involucres.

Ceramium marshallense also bears some resemblance to Setchell and Gardner's (1937) *C. templetonii*, described from the Galapagos Islands, agreeing with

that alga in its diminutive size (only a few mm tall), diameter of the axes (to 110 μm), dichotomous branching, and strongly forcipate apices. In that species, however, tetrasporangia are produced in whorls of 4–6, are tetrahedrally divided, and are larger (55–65 μm in diameter). Another species with a small size, dichotomous branching, and whorled tetrasporangia is *C. nakamurai* Dawson (Nakamura 1950, as *C. equisetoides*, nom. illeg.], but this species has thalli with erect, non-forcipate apices and exceedingly swollen tetrasporangial nodes.

Delesseriaceae

Hypoglossum simulans Wynne, I. Price & Ballantine.

Collections: 4D-2 (♀); 4F-14 (♂, ⊕).

A number of small thalli were retrieved from coral pieces and *Halimeda*, and although fragmentary, these plants show several of the features shared with *Hypoglossum simulans*: a decumbent habit owing to the sporadic production of rhizoids from marginal cells; branches originating from basal segment of the parent blade; an ecorticate midrib; and an apical organization in which not all cells of second-order rows bear third-order rows. This species was described from Wynne et al. (1989) on the basis of a type from the Guadeloupe, French West Indies, in the Caribbean. At the same time they also reported its occurrence from eastern Australia, the South Pacific, and Hawaii.

Martensia fragilis Harvey.

Collection: 4D-13.

This determination is based on a single vegetative specimen, lacking the distinctive meshwork characteristic of this genus. Yet morphological evidence strongly support this identification. The blade has a marginal meristem of initials, minute marginal teeth or denticulations, and tufts of marginal rhizoids for attachment, features consistent with the figures of *Martensia fragilis* given by Svedelius (1908, figs. 4, 20, 28). Additionally, *M. fragilis* was described by Harvey (1854) from Sri Lanka. According to Millar (1990), *M. denticulata* Harv., described by Harvey (1855) from Western Australia, and *M. pavonia* (J. Ag.) J. Ag., described by J. Agardh (1854, as *Mesotrema pavonica*) from Guadeloupe in the West Indies, should be regarded as conspecific with *M. fragilis*.

Dasyaceae

Heterosiphonia crispella (C. Agardh) Wynne var. **laxa** (Børgesen) Wynne.

Collection: 4C-2 (⊕).

Both varieties of this species are commonly distributed in tropical and subtropical seas around the world (Wynne 1985b). The soft, decumbent form and the occurrence of four pericentral cells per segment allow the determination of this collection as var. *laxa*.

Rhodomelaceae

Chondria curvilineata Collins & Hervey.

Collection: 4F-7 (⊕).

The axes are branched to two orders and are soft and slender, measuring 0.28–0.36 mm in diameter. First described from Bermuda (Collins & Hervey 1917),

Chondria curvilineata has also been reported from the Caribbean (Taylor 1960), North Carolina (Schneider & Searles 1991), and the Philippines (Meñez & Calumpong 1981). Two prominent features that support this determination are the truncate ultimate branches with the growing points located in an apical depression (subg. *Coelochondria*) and the conspicuous end walls of pericentral cells. In this collection from the Maldives, however, it is the proximal walls of the pericentral cells that have the caplike thickenings; the distal walls of some but not all pericentral cells are also thickened but not to the degree as the proximal walls. Collins and Hervey (1917) described only the distal ends of the pericentral cells to be conspicuously thickened in *C. curvilineata*. Gordon-Mills & Womersley (1987) discussed two modes of initiation of cell wall thickenings in *Chondria*. The first is as a single thickening on the upper (i.e., distal) side of the radially elongate pericentral cells and the second is as two thickenings, each on the radial walls of the pericentral cell, but they did not refer to a pattern in which the lower (i.e., proximal) walls of the pericentral cells were conspicuously thickened. An examination of an isotype of *C. curvilineata* in MICH (*P. B.-A. No. 2039*) revealed that the upper walls did bear caplike thickenings just as Collins and Hervey (1917) described, but the proximal walls also bore refractive caps, though less conspicuously expressed than the distal walls. The conclusion is that this is a variation within *Chondria curvilineata*.

The Maldivian material shows a tendency to be creeping, with holdfasts produced sporadically over the axes. There is thus some resemblance in its habit to *Chondria repens* Børgesen, a species described from Easter Island (Børgesen 1924) but now known to have a broad tropical range (Dawson 1954a; Cordero 1977; Cribb 1983). That species is like *C. curvilineata* in having the same kind of sunken apex. The thick cortical layer, the non-evident nature of pericentral cells, and the lack of a clear axial row in *C. repens* all point to its closer affinity with *Laurencia*, as earlier suggested by Gordon-Mills and Womersley (1987). Two other species, namely, *C. minutula* Weber-van Bosse (1923) and *C. polyrhiza* Collins & Hervey (1917), bear some resemblance to the Maldivian material in general habit, but these species have exserted apices and lack the caplike thickenings of the pericentral cells.

Herposiphonia secunda (C. Agardh) Ambronn f. **tenella** (C. Agardh) Wynne.

Collection: 4F-8.

This material has 8 pericentral cells per segment, with almost all segments of the indeterminate axes bearing either a determinate or an indeterminate branch (or primordium of an indeterminate branch), and with 1–2 usually poorly developed branched trichoblasts terminating the determinate branches. Indeterminate axes are 68–86 μm broad, and determinate axes are 38–44 μm broad. The determinate branches of these plants usually consisted of 12 segments. Hollenberg (1968b) presented the evidence for regarding *H. secunda* and *H. tenella* as conspecific, maintaining one as a forma of the other. Wynne (1985a) pointed out that *H. secunda* predates *H. tenella*.

Laurencia carolinensis Saito.

Collection: 4B-13.

The following features are evidence for this determination: clump-forming thalli, 3 cm tall, made up of cartilaginous, terete axes, which are branched in all directions and interlocking among themselves. Axes average 1250–1400 μm in diameter. A stoloniferous system is lacking. Indeterminate branches give rise to many short determinate branches, especially in the upper portions of the thallus,

as shown by Saito (1969, fig. 7A). Superficial cortical cells lack secondary pit-connections and are not radially elongate in transverse section, but these superficial cortical cells project above the surface of the thallus. Saito (1969) described this species from the Caroline Islands.

Laurencia dotyi Saito.

Collections: 4B-26; 4D-10 (⊕).

This species was described from the Hawaiian Islands by Saito (1969). It lacks secondary pit-connections between the superficial cortical cells (subg. *Chondrophycus*). Other characters include compressed, percurrent axes with distichous branches, arising both alternately and oppositely, and prominently projecting but not radially elongated superficial cortical cells. Tetrasporangia are produced near the apices in whorls in a perpendicular arrangement.

Laurencia majuscula (Harvey) Lucas.

Collection: 4B-16.

Several features relate this collection to sect. *Laurencia* of subg. *Laurencia*: secondary pit-connections present between epidermal cells, terete axes, and lenticular thickenings in walls of medullary cells. Within that section, the projecting nature of cortical cells points to a determination as *L. majuscula* (Saito 1969). This species is now recognized to have a wide Indo-Pacific distribution, including Western Australia (the type locality), Hawaii, the Philippines, and southern Japan.

Laurencia parvipapillata Tseng.

Collection: 4E-28.

This species is of small stature, with rigid, cartilaginous compressed axes (0.8 mm in diameter) that bear distichously arranged knoblike branchlets. Tetrasporangia are formed in a perpendicular arrangement (Tseng 1943). The habit is caespitose. Epidermal cells are radially elongate in transverse section of the axes (Saito 1969) and also strongly mammilate. Zhang and Xia (1985) depicted Chinese material of this species and agreed with Saito's (1969) assignment of it to sect. *Palisadae* in subg. *Chondrophycus* rather than with Tseng's (1943) original assignment of this species in sect. *Pinnatifidae* in subg. *Laurencia*.

Laurencia tenera Tseng.

Collections: 4B-30; 4D-8 (⊕); 4E-29.

Evidence for the identification of this collection as *Laurencia tenera* include the small stature of the thallus (to 7 mm tall), the narrow breadth of terete axes (320–600 μm), the soft texture of the thallus, and the size of epidermal cells (20–30 μm in surface diameter). Additionally, hapteroidal side branches are produced at right angles to parent axes, which interlock the branches and result in a caespitose habit. Tetrasporangia show a parallel arrangement, as figured by Tseng (1943). The presence of secondary pit connections between the epidermal cells and the absence of lenticular thickenings in walls of medullary cells are in agreement with observations made by Saito (1969). One discrepancy noted in coll. 4D-8 with other accounts is that the outer surfaces of epidermal cells in young axes are mammilate; these projections are not so evident in older axes.

This species was first described from Hong Kong (Tseng 1943) and has also been recorded from Vietnam (Dawson 1954a), Hawaii (Saito 1969), and Tanzania (Jaasund 1976).

Laurencia undulata Yamada.

Collection: 4B-28 (⊕).

This alga consists of a caespitose clump of flattened axes with a softly fleshy texture in agreement with the account of this species by Tseng (1943). Main axes are about 3 cm tall and 2–3 mm broad; branches were reported to be 5 mm broad by Yamada (1931) and 4 mm broad by Tseng (1983). Branches arise distichously, resulting in a complanate habit. Even the final branches are flattened. Ultimate branches are slightly upcurved with their apical region tucked into a depression on the upper surface of the axis. Superficial cortical cells lack secondary pit-connections and are usually subquadrate, but occasionally slightly radially elongated. Refractive wall thickenings of the medullary cells are absent. Tetrasporangia are produced close to the apices of the frond and show a perpendicular arrangement.

Originally described from Enoshima, Japan (Yamada 1931), *Laurencia undulata* has been reported from China (Tseng 1943, 1983), Hawaii (Saito 1969), and the Philippines (Cordero 1977). Tseng et al. (1980) stated that it is one of the more common species of *Laurencia* in Hong Kong. *Laurencia undulata*, assigned to subg. *Chondrophycus* (Saito 1967), bears some resemblance to *L. parvipapillata* Tseng and *L. succisa* Cribb in its habit of flattened axes with distichous branches. Fronds of *L. parvipapillata*, however, are very cartilaginous rather than softly fleshy (Tseng 1943), and its surface cells are conspicuously protruding. Fronds of *L. succisa* are also cartilaginous and rigid, and the final branchlets are cylindric to cylindrico-clavate (Cribb 1958, 1983).

Polysiphonia japonica Harvey var. **savatieri** (Hariot) Yoon.

Collection: 4H-1 (♂, ♀, and ⊕).

According to Yoon (1986), this variety of *Polysiphonia japonica* is characterized by its relatively small thallus size (only 0.5–1.0 cm tall) and ecorticate axes (in contrast to the 5 cm height and corticated basal portions of var. *japonica*), regular dichotomous branching, trichoblasts being formed from each segment, the tetrasiphonous condition, attachment by a dense aggregation of unicellular rhizoids, rhizoids cut off from pericentral cells, and broadly globose cystocarps with a wide ostiole. This species is now recognized to have a wide geographical distribution including Japan and Korea, Pacific North America (Abbott & Hollenberg 1976), the Philippines (Silva et al. 1987), and the Seychelles (Wynne, submitted-B).

Polysiphonia setacea Hollenberg.

Collection: 4C-9 (⊕).

These thalli were of a small stature and creeping over rock substratum. There are four pericentral cells per segment and no cortication. Although trichoblasts are rarely produced, a small scar cell is cut off one per segment in a 1/4 spiral sequence. A distinctive trait of this species is the production of numerous rhizoids, which are cut off by a cross–wall from pericentral cells at their extreme distal end; these rhizoids arise all along these axes, resulting in the creeping habit. Each rhizoid is at first unicellular but later produces an elaborate, multicellular discoid attachment pad, in agreement with Hollenberg's (1968a) depiction. Hollenberg (1968a) listed numerous records of this species throughout the tropical Pacific Ocean as well as from Atlantic Central America. Also, in the opinion of Oliveira F. and Cordeiro–Marino (1970), Collins and Hervey's (1917) original

description of *Lophosiphonia bermudensis* (from Bermuda) was based on a mixture of three taxa, including *P. setacea*.

Tolypiocladia glomerulata (C. Agardh) Schmitz in Schmitz & Hauptfleisch.
Collection: 4B–29.

Phaeophyta

Ectocarpales

Ectocarpaceae

Hincksia breviarticulata (J. Agardh) Silva.
Collection: 4E–2.

Sphacelariales

Sphacelariaceae

Sphacelaria sp.
Collection: 4C–10.
Propagules were absent.

Dictyotales

Dictyotaceae

Dictyota adnata Zanardini *prox.*
Collection: 4B–31.

Coppejans (1990) redefined the concept of Zanardini's ill-known *Dictyota adnata*, restricting it to a *Dictyota* with prostrate growth, attached by marginal groups of rhizoids, and the restriction of the sporangia to marginal sori. Also, both cortical and medullary cells are relatively large and have relatively high cell ratios. Thus, Jaasund's (1970) record of *D. adnata* from Tanzania, in which he depicted it as being bluish green-iridescent and with sori of sporangia occurring on the entire blade surface, was discounted. Hörnig et al. (1992) agreed that living and dried specimens of genuine *D. adnata* are brown. They assigned previous Caribbean records of *D. adnata* to their new species *D. humifusa*.

The Seychellois plants are prostrate growths (epiphytic on *Laurencia*), 10–16 mm long and 1.5–3.0 mm broad [which is somewhat greater than the breadth reported by Coppejans (1990)], with marginal rhizoids. Because the material is sterile and was found growing in a coral reef rather than in a mangrove habitat, its identification is tentative.

Fucales

Sargassaceae

Turbinaria luzonensis W. R. Taylor.
Collection: 4B-23.

Chlorophyta

Ulvales

Ulvaceae

Enteromorpha clathrata (Roth) Greville.

Collection: 4H-3.

These small thalli are abundantly branched throughout, with both uniseriate and multiseriate branches, in agreement with Dawson's (1954a) account of this species.

Enteromorpha lingulata J. Agardh.

Collection: 4E-23 (epiphytic on *Gelidiopsis intricata*).

The plants of this species are also small, barely reaching 10 mm in height, but unlike in *Enteromorpha clathrata* the branches are uniformly multiseriate. Branches are approximately the same diameter as that of primary axes.

Cladophorales

Cladophoraceae

Cladophora vagabunda (Linn.) van den Hoek.

Collection: 4H-2.

The dense nature of the branching and the curved final branches caused me to make an initial identification of this alga as *Cladophora mauritiana* Kützing, as depicted by Børgesen (1946) and Jaasund (1976). However, according to van den Hoek (1963, 1982), *C. mauritiana* should be regarded as a taxonomic synonym of *C. vagabunda*, and his view is accepted here.

Siphonocladales

Siphonocladaceae

Boodlea composita (Harvey) Brand.

Collection: 4E-6.

This alga forms a spongy, reticulate thallus, which has three-dimensional branching. Hapteroid segments fuse branch apices to other branches, resulting in a congested cushion. Cribb (1960) and Egerod (1975) listed *Boodlea siamensis* Reinbold and *B. kaeneana* Brand as taxonomic synonyms of *B. composita*. This species is widely distributed in tropical waters of the Indian and Pacific Oceans (Egerod 1952).

Cladophoropsis sundanensis Reinbold.

Collection: 4C-6.

Dictyosphaeria versluysii Weber-van Bosse.

Collection: 4E-21.

Struvea anastomosans (Harvey) Piccone.

Collections: 4C-5; 4D-1.

These plants of *Struvea* are uniformly small, the primary stalk and its blade(s) attaining heights of only 7–20 mm. The stalk is either simple, bearing a single blade, or branched, bearing up to three blades; it is usually non-segmented, but in one plant the stalk is segmented. The lack of annular constrictions in the stalk precludes assignment to several species in the genus (Egerod 1952). *Struvea pulcherrima* (J. E. Gray) Murray & Boodle can be ruled out because of the much larger size of its blades. This collection is assigned to *S. anastomosans*, which includes *S. tenuis*. The latter taxon was described by Zanardini (1878) from Soroñg, Papua New Guinea, and distinguished on the basis of its bipinnate blades and its relatively small size. It has been depicted by Murray and Boodle (1888, fig. 5). Initially, Egerod (1952) accepted *Struvea tenuis*. She regarded it as an exceedingly small plant with a bipinnate blade. However, in eastern Australian material of *S. anastomosans,* Cribb (1960) observed considerable variation in the size and form of the frond and also in regard to the method of frond formation, and thus he thought it likely that *S. tenuis* was conspecific with *S. anastomosans*. On the basis of the range of form seen in their Solomon Islands material, Womersley and Bailey (1970) regarded Cribb's taxonomic view as likely. Egerod (1975) also came to accept this view. I have followed this taxonomic decision to regard *S. tenuis* as a taxonomic synonym of *S. anastomosans*.

Pilger (1920) recognized *Struvea multipartita*, separating it from *S. anastomosans* because of the irregular branching of the nets and their small size. Steentoft (1967) thought that *S. multipartita* was only a growth form of *S. anastomosans*, and Lawson and John (1982) later concurred with that taxonomic opinion. Thus, *S. anastomosans* is considered here to be a morphologically somewhat variable taxon with a pantropical distribution.

Two other species of *Struvea* were described by Gepp and Gepp (1908) from the central and western Indian Ocean, namely, *S. gardineri* from Cargados Carajos and *S. orientalis* from Amirante Islands, which lie to the west of the Seychelles. These two species seem to be recognized only from their original accounts.

Ventricaria ventricosa (J. Agardh) Olsen & West.

Collection: 4F-2.

Caulerpales

Bryopsidaceae

Bryopsis indica Gepp & Gepp.

Collection: 4D-4.

This species was described by Gepp and Gepp (1908) from various localities in the Indian Ocean, including Chagos Archipelago. A distinctive feature is that the branching appears to be distichous, but each row is made up of two slightly offset, irregular rows of ramuli, as depicted by Gepp and Gepp (1908, pl. 22, fig. 11). After ramuli are shed, scars remain revealing this pattern. Womersley and Bailey (1970) discussed the relationship of *B. indica* to the similar *B. australis* Sonder from Western Australia and the pantropical *B. pennata* Lamouroux, the latter species having been reported from the Maldives by Tsuda and Newhouse (1966). According to Womersley and Bailey (1970), it is probable that in the Indo-Pacific region there has been confusion between *B. indica* and *B. pennata*, some material having been referred to both species.

Codiaceae

Codium geppiorum O. C. Schmidt.
Collection: 4C-1.
This collection was determined by Dr. P. C. Silva.

Caulerpaceae

Caulerpa racemosa (Forsskål) J. Agardh var. **peltata** (Lamouroux) Eubank.
Collection: 4B-7.
The fact that at least three of the "varieties" (var. *peltata*, var. *turbinata*, and var. *laetevirens*) of this widespread and morphologically variable species form a continuum has been reiterated by Coppejans and Beeckman (1989). Furthermore, Ohba and Enomoto (1987) showed by culturing experiments involving variations in light intensity and temperature that the var. *peltata*-type assimilator or the var. *laetevirens*-type assimilator could be formed at will. This evidence supports the taxonomic conclusion of Eubank (1946) to place *C. peltata* Lamouroux at the varietal level within *C. racemosa*. The varietal epithet *peltata*, of *Fucus chemnitzia* [var.] *peltatus* (Lamouroux) Turner (1819), has priority.

Caulerpa racemosa (Forsskål) J. Agardh var. **turbinata** (J. Agardh) Eubank.
Collection: 4E-7.

Udoteaceae

Chlorodesmis hildebrandtii A. Gepp & E. S. Gepp.
Collection: 4D-3.
This collection was identified by S. Ducker and included in her monographic treatment of this genus (Ducker 1967).

Halimeda fragilis W. R. Taylor.
Collections: 4B-17; 4D-14.
Primary utricles measure 12–22 μm in surface diameter, which is somewhat less than the 21–52 μm range given by Hillis-Colinvaux (1980). *Halimeda fragilis* has some similarities with *H. opuntia*, including the compact, cushionlike habit and the utricles being in the same size range in surface view. But the utricles of *H. fragilis* have a rounded shape in surface view rather than polygonal, and nodal medullary siphons are unfused with noticeably thickened walls in this region. Hillis (1959) reported *H. fragilis* from Cargados Carajos in the Indian Ocean.

Halimeda micronesica Yamada. Fig. 10.
Collection: 4F-10.
One of the most distinctive features of *Halimeda micronesica* is the single attachment basal segment, which is conspicuously enlarged and broadened, giving rise to numerous erect branches (Yamada 1941, 1944a). In *H. melanesica* Valet (1966) and *H. renschii* Hauck (1886; Hillis-Colinvaux 1980) the basal region is comprised of several adherent segments, giving a stalklike appearance. Another characteristic of *H. micronesica* is that the primary utricles are rounded in surface view (Fig. 10), measuring about 26–40 μm in diameter; they easily dissociate on decalcification. An additional distinctive feature present in this collection is the

occurrence of stolonlike runners asexually giving rise to new plants. These fibrous runners are made up of multiaxial rhizoidal filaments. This appears to be the first record of this species from the Maldives; Hillis (1959) has reported it from the Seychelles.

Halimeda opuntia (Linnaeus) Lamouroux var. **opuntia.** Fig. 11.

Collection: 4B-18; 4E-14.

This species occurred in abundance in the shallow reef flats, forming three-dimensional compact clumps. Rhizoids can be produced wherever it comes into contact with substratum. Peripheral utricles measured 20–28 μm in surface diameter, which is consistent with the values given by Hillis-Colinvaux (1980) and Tsuda and Kamura (1991).

Halimeda taenicola W. R. Taylor. Fig. 12.

Collection: 4B-9.

The habit of *Halimeda taenicola* is erect and compact. This species is distinguished by the following distinctive features: a single basal segment for attachment, moderately heavy calcification, nodal medullary filaments fused in two and threes, relatively enlarged tertiary utricles, and primary utricles that are polygonal, 40–56 μm diameter, and occasionally fused in surface view. Taylor (1950) described this species from Bikini Atoll in the Marshall Islands. Hillis-Colinvaux (1980) indicated that it was distributed in the northern and southern Western Pacific Ocean; South (1992) reported its occurrence at Fiji in the South Pacific. This report from the Maldives appears to be the first record from the Indian Ocean.

Halimeda tuna (Ellis & Solander) Lamouroux. Fig. 13.

Collections: 4B-22; 4F-4.

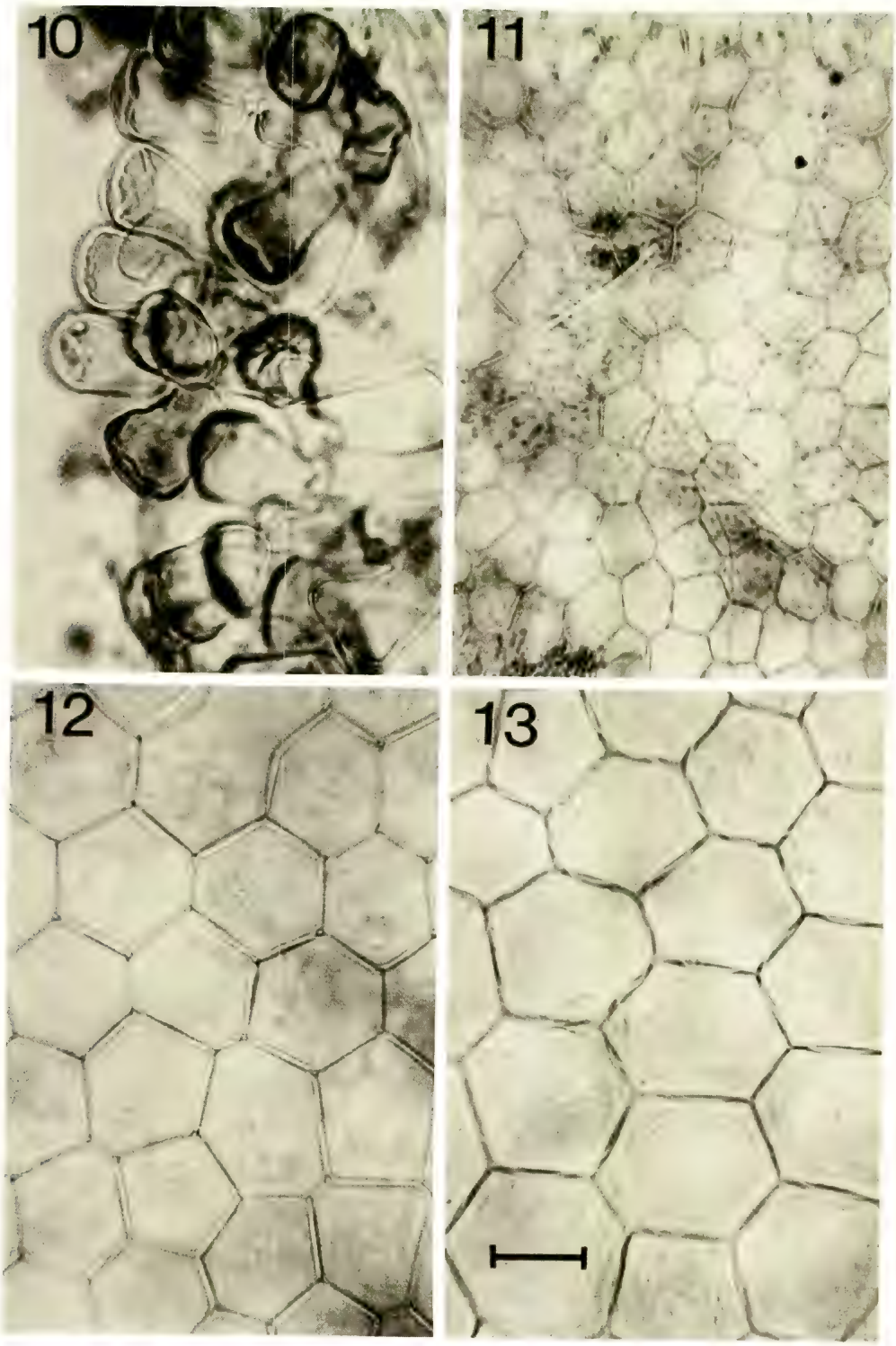
The plants form laxly branched, three-dimensional clumps, which are attached to the substratum by a single segment. The segments, which are ovate to reniform and lightly calcified, are 4–6 mm broad and 3–4 mm tall, but segments at points of branching are broader. Upon decalcification the primary utricles remain strongly attached and are polygonal in outline. Primary utricles measure 40–50 (–60) μm in surface diameter. The utricles are conspicuously constricted at their bases, in agreement with the description in Hillis-Colinvaux (1980).

Halimeda copiosa Goreau & Graham is an additional species of the genus collected from the Maldives by H. E. Hackett and reported by Colinvaux (1968, as *H. hederacea*), but it was not encountered in the present collections.

Rhipidosiphon javensis Montagne. Fig. 14.

Collection: 4B-14.

Littler and Littler (1990) have recently reinstated Montagne's (1842) *Rhipidosiphon*, mainly on the basis of its few derived characteristics relative to other species of *Udotea*. Gepp and Gepp (1904, 1911) had regarded *Rhipidosiphon* as the "simplest form" of *Udotea* and merged the two genera. A single thallus was observed (Fig. 14a). It has a unistratose blade attached to a monosiphonous stalk. The blade is composed of dichotomously branched contiguous siphons with slightly off-set constrictions (Fig. 14b). The siphons are held together by calcification. The stipe, however, lacked calcification; this observation concurs with that of Gepp



FIGS. 10–13. *Halimeda*. Surface view of cortex. Fig. 10. *H. micronesica*. Fig. 11. *H. opuntia*. Fig. 12. *H. taenicola*. Fig. 13. *H. tuna*. Scale bar = 50 µm.

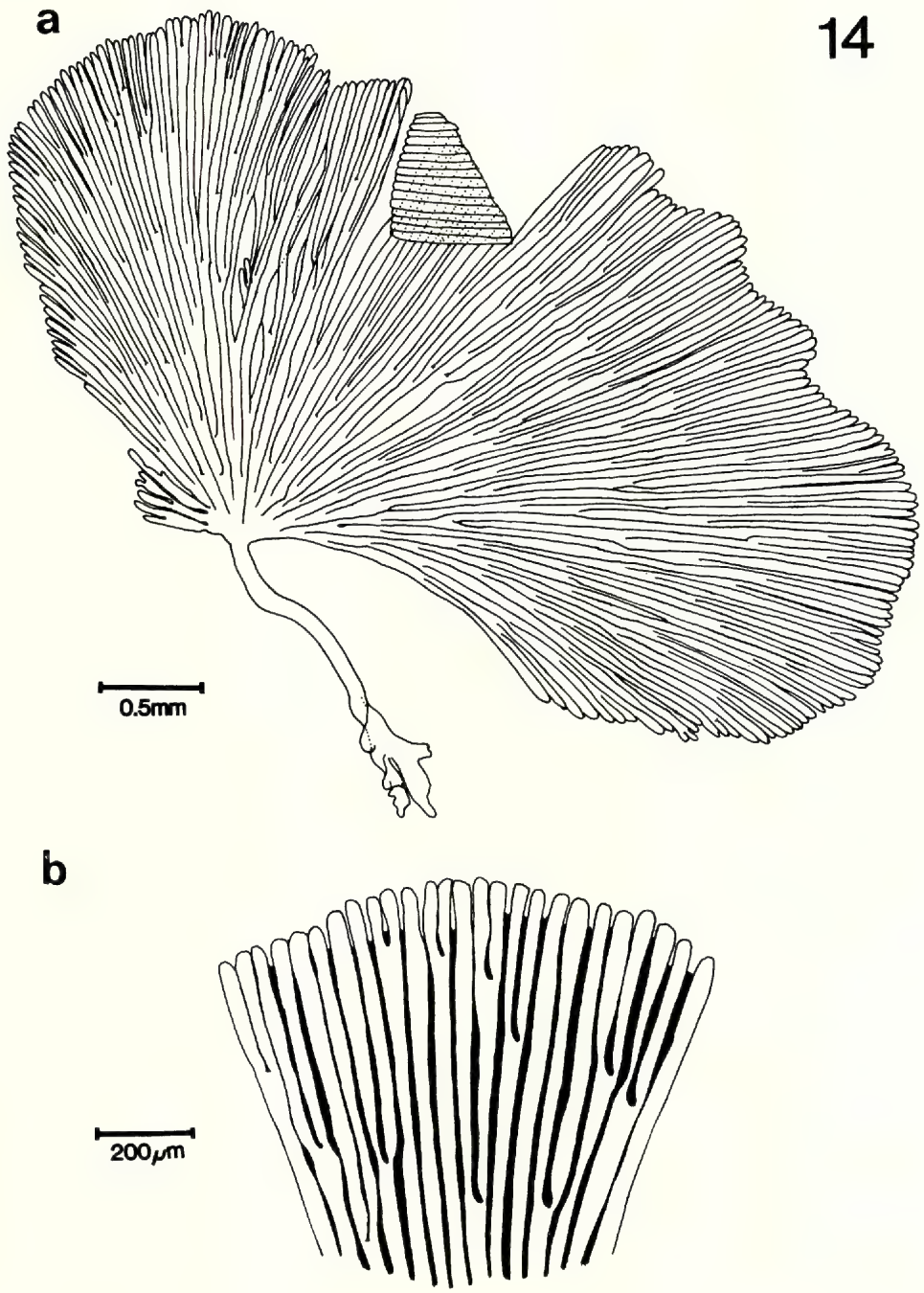


FIG. 14. *Rhipidosiphon javensis*. a, thallus composed of a monosiphonous stalk and a unistratose blade made up of dichotomously branched siphons; b, detail of blade showing slightly offset dichotomies of siphons, held together by calcification.

and Gepp (1904, 1911) but not with that of Littler and Littler (1990). Egerod (1952) noted that Hawaiian plants of this alga were often noncalcified. Siphons are 34–40 μm in diameter, a range slightly less than the 40–50 μm range reported by Gepp and Gepp (1911) and Littler and Littler (1990). This species is known to be widely distributed throughout the Indo-Pacific (Egerod 1952). It was previously reported from the Maldives by Littler and Littler (1990).

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APPENDIX

Collection sites in the Maldives

4A: Dunidu Island; 5.xi.1964; 1 m depth, on boulders in shade below pier.
4B: Funidu Island, north of Mále; 5.xi.1964; 1 m depth, coral reef area.
4C: Hulele Island, east side of island; 6.xi.1964; boulder reef area.
4D: Funidu Island, north of Mále; 6.xi.1964.
4E: Hulele Island, east side of island; 7.xi.1964; exposed rocky flats below boulder ridge.
4F: reef lagoon area north of Hulele Island; 7.xi.1964; protected area.
4G: reef edge of Hulele Island; 7.xi.1964.
4H: Hulele Island, north side of island, seagrass flats near shore; 7.xi.1964.

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NEW TAXA AND NOMENCLATURAL CHANGES IN THE NORTH AMERICAN FERN FLORA

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The ferns represent an ancient and diverse lineage in which hybridization and reticulate evolution have been extraordinarily common. Although the phylogenetic history of some fern genera can be reconstructed accurately from traditional morphological studies (e.g., *Osmunda*; see Miller 1971), the majority did not begin to yield their evolutionary secrets until the advent of experimental systematics less than 50 years ago (see Manton 1950). A combination of chromosome and isozyme analyses has proven to be one of the most effective tools in fern systematics (Haufler 1985), providing insights into the phylogenetic histories of many, seemingly intractable groups. A number of these studies by myself and my colleagues have been published (e.g., Windham 1987a; Paris & Windham 1988; Gastony & Windham 1989; Haufler & Windham 1991), but analyses done in the last few years have not yet appeared in print. These unpublished studies indicate the need for significant taxonomic changes in several North American fern genera. The following overview of new taxa and nomenclatural changes is presented to expedite the treatment of these genera in *Flora of North America*, *Vascular Plants of Arizona*, and other ongoing floristic projects.

Argyrochosma

When *Argyrochosma* was first recognized as a genus distinct from *Notholaena* (Windham 1987a), only those names in use at the species level were transferred to the new genus. Previous authors (e.g., R. Tryon 1956) had recognized infraspecific taxa in several species, but the transfer of these names to *Argyrochosma* was delayed pending a more thorough review of systematic relationships in the genus. That review is not yet complete, but the impending publication of *Flora of North America* requires that a decision be made concerning the status of infraspecific taxa within *Argyrochosma limitanea* (Maxon) Windham. This species includes two morphologically distinctive taxa that show significant differences in blade shape and degree of dissection. The typical form of *A. limitanea* has broadly ovate-deltate leaf blades that are 4–5-pinnate, with the basal pinnae at least 1/2 as long as the blades. The taxon herein called subsp. *mexicana* has lanceolate to oblong leaf blades that are 3–4-pinnate, with basal pinnae that are 1/4 to 1/3 as long as the blades. These taxa tend to occupy different geographic ranges (R. Tryon 1956; maps 55, 56), and genetic interaction between them in regions of sympatry is precluded by the fact that both are apogamous triploids. Isozyme analyses indicate that the two taxa have different polyploid origins and may be worthy of recognition at the species level. However, evolutionary relationships (and thus proper taxonomic treatment) cannot be resolved until the sexually-reproducing progenitors of these polyploids are found. In the interim, these taxa

are best recognized as subspecies of *A. limitanea*, and the following new combination is proposed.

Argyrochosma limitanea (Maxon) Windham subsp. **mexicana** (Maxon) Windham, comb. nov. *Notholaena limitanea* subsp. *mexicana* Maxon, Amer. Fern J. 9: 72. 1919.—TYPE: MEXICO. Chihuahua: Santa Eulalia Mts, 15 Sep 1885, *Pringle 451* (holotype: US!).

CHEILANTHES

During detailed monographic studies of *Cheilanthes* subgenus *Physapteris*, Reeves (1979) ascertained that there were two distinct species included within *Cheilanthes wootonii* Maxon. As Reeves observed, typical representatives of *C. wootonii* have leaf blades that appear glabrous adaxially, abaxial blade scales that are often ciliate only in the proximal half, and rhizome scales that are usually light brown and deciduous on older portions of the rhizome. The taxon Reeves provisionally called *C. yavapensis* was distinguished by having leaf blades that appear sparsely pubescent adaxially, abaxial blade scales that are ciliate for most of their length, and rhizome scales that are dark brown (or bicolorous with a dark central stripe) and persistent. Initial reports (Reeves 1979) that *C. wootonii* and *C. yavapensis* are distinguished by the number of spores per sporangium have proven incorrect, but subsequent analyses have revealed genetic distinctions that reinforce the recognition of two species. Chromosome studies of *C. wootonii* s.s. indicate that this taxon is an apogamous triploid with $n = 90$ (Windham 1983). *Cheilanthes yavapensis*, on the other hand, has proven to be an apogamous tetraploid with $n = 120$. A correlation between chromosome number and spore size provides an additional morphological character distinguishing *C. wootonii* (spores averaging < 64 µm long) from *C. yavapensis* (spores averaging > 64 µm long). Although the origin of triploid *C. wootonii* is uncertain, isozyme studies suggest that *C. yavapensis* arose through hybridization between *C. lindheimeri* Hooker (an apogamous triploid quite distinct from *C. wootonii*) and the sexual diploid known as *C. covillei* Maxon (Gastony & Windham 1989). These studies clearly indicate that *C. wootonii* was not involved in the polyploid origin of *C. yavapensis*, and that the similarities between these taxa result from hybrid convergence rather than common ancestry. The distinctive nature of Reeves' *C. yavapensis* is thus confirmed and his manuscript name is here validated.

Cheilanthes yavapensis Reeves ex Windham, sp. nov.—TYPE: U.S.A. Arizona: Yavapai Co., small east-wall tributary of Black Canyon at a point 3.09 km SSW of Sheep Gulch Spring and 1.13 km NE of the confluence of Black Canyon and Sycamore Creek, 2485 ft, 18 Nov 1980, *Windham 202* (holotype: UT!; isotypes: ASC! ASU! US!). Fig. 1.

C. wootonii Maxon similis, a qua differt laminarum paleis abaxialibus ciliatis fere per longitudinem, segmentis ultimis minoribus adaxaliter pilis dispersis ramosis instructis, laminis ut videtur pubescentibus adaxialiter, paleis rhizomatum furvioribus magis persistentibus, sporis plus quam (x) = 64 µm longis metientibus, chromosomatum numero $n = 120$; a *C. lindheimeri* Hooker differt laminis ut videtur sparsim (non dense) pubescentibus adaxialiter, paleis abaxialibus laminarum

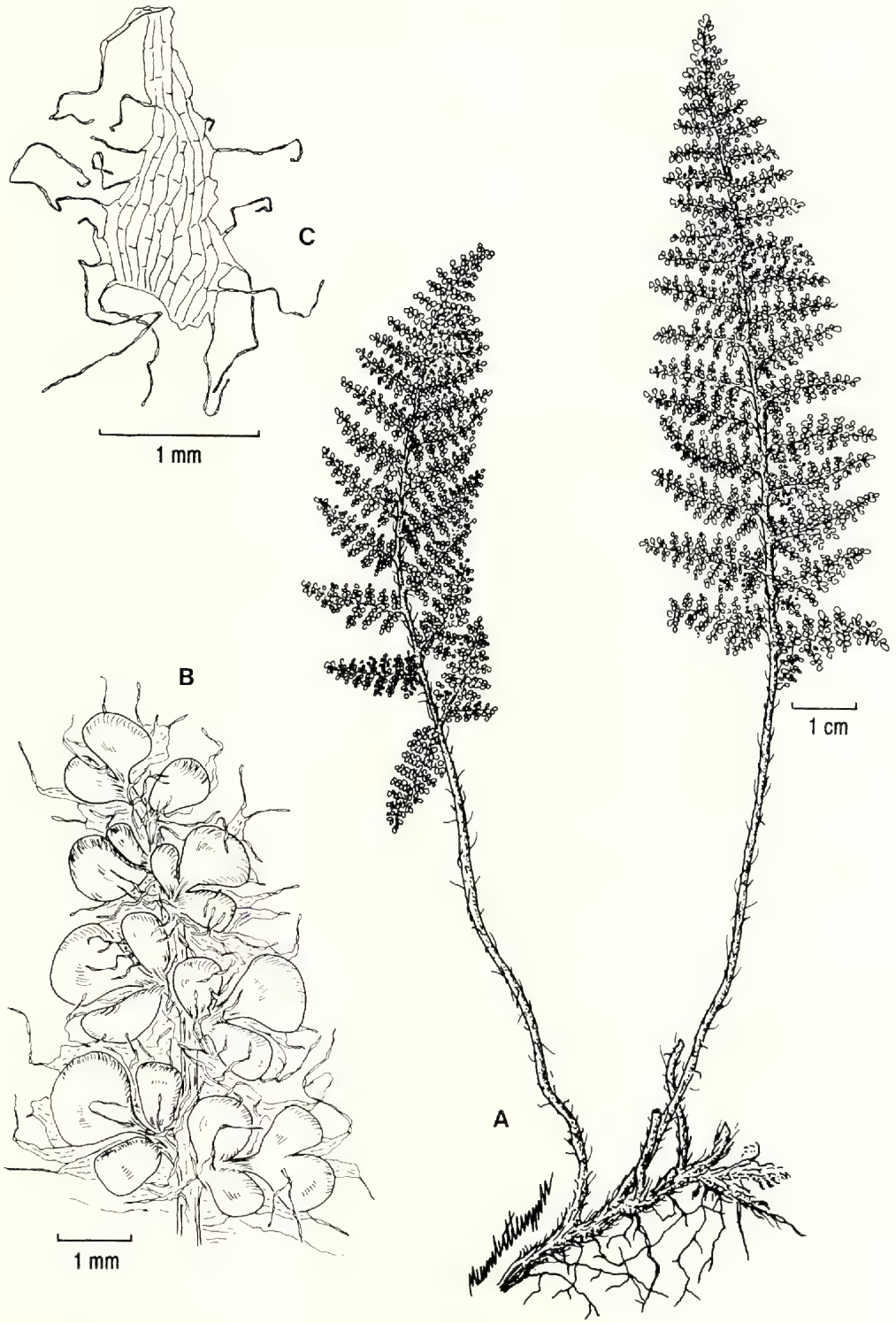

FIG. 1. *Cheilanthes yavapensis*. A. Habit. B. Adaxial view of pinnule; note overtopping cilia of abaxial costal scales and occasional branched hairs that make leaf appear pubescent. C. Abaxial costal scale; note cilia distributed entire length of scale. (Based on *Windham (787) & Yatskievych.*)

ciliis grossioribus, his non valde intricatis, segmentis ultimis plus quam 1 mm in diametro, rhizomatum paleis brunneis valde appressis magis persistentibus, sporis plus quam (x) = 64 μm longis metientibus, chromosomatum numero $n = 120$.

Plants epipetric. Rhizomes usually long-creeping, 1–3 mm in diameter; rhizome scales lanceolate, strongly appressed, persistent, often bicolorous with a broad, poorly defined, dark brown central stripe and narrow, pale brown margins. Leaves 7–35 × 2–6 cm, scattered along rhizome; croziers non-circinate, hooked. Petioles dark brown, rounded adaxially. Blades oblong-lanceolate to nearly ovate, 4-pinnate proximally; rachises rounded adaxially, with scattered linear-lanceolate scales and sparse monomorphic pubescence. Pinnae appearing sparsely pubescent adaxially, the basal pair not conspicuously larger than adjacent pair, more or less equilateral; costae green adaxially for most of their length; abaxial costal scales lanceolate, the largest 0.4–1.0 mm wide, truncate to cordate at base, without overlapping basal lobes, strongly imbricate and often concealing ultimate segments, with coarse cilia usually distributed entire length of scale. Ultimate segments round to oblong, beadlike, the largest usually 1–2 mm; abaxial surface glabrous or with a few small scales near base; adaxial surface nearly glabrous except for occasional branched hairs; segment margins recurved to form weakly differentiated false indusia. Sporangia containing 32 spores. Spores averaging 64–72 μm long. Chromosome number: $n = 120$ (from the holotype population and paratypes indicated by *).

Distribution. U.S.A., Arizona, southern New Mexico, and Trans-Pecos Texas; rocky slopes and ledges, usually on igneous substrates; 500–2400 m.

Paratypes. **U.S.A.** Arizona: Coconino Co., at base of massive lava flow on the SE slope of Elden Mountain, *Windham (589) & Czech** (ASC, UC); Gila Co., southwest wall of Sand Tank Canyon in the Sierra Ancha, *Windham (787) & Yatskievych** (BRY, UT); Graham Co., along small tributary of Jacobson Canyon in the Pinaleno Mts, *Windham (775) & Yatskievych* (ARIZ, UT); Maricopa Co., cliff above lower Dripping Springs Canyon, White Tank Mountains Regional Park, *Keil 6297* (ASU, MEXU, UNM); Yavapai Co., Bradshaw Mts, midway between Cleator and Crown King, *Lehto 23641* (ASU).—New Mexico: Grant Co., along small tributary of Sawmill Canyon in the Big Burro Mts, *Windham (769) & Yatskievych* (NMC, UT, UTC, UTEP).

Notholaena

Notholaena californica D. Eaton comprises white and yellow color morphs that show striking differences in the chemical composition of the powdery farina concentrated on abaxial leaf surfaces (Wollenweber 1984). The chemical distinctions between the color morphs were so profound that Wollenweber considered *N. californica* one of the best candidates in *Notholaena* for the recognition of infraspecific taxa. Subsequent chromosome studies further reinforce the differences between the white and yellow morphs. Preliminary data indicate that the white morph consists of sexual diploids and low polyploids (apogamous triploids and possibly tetraploids), whereas the yellow morph appears to consist entirely of high polyploids (apogamous pentaploids). The two color morphs are rarely, if ever, found growing at the same locality, and gene flow in the region of sympatry (southern California) is prevented because both are apogamous in this area. These taxa ultimately may prove worthy of recognition as distinct species, but until the complex evolutionary history of the group is resolved subspecific status seems

most appropriate. The lectotype of *N. californica* (chosen by R. Tryon 1956) and the holotype of the only previously recognized subspecies (*N. californica* subsp. *nigrescens* Ewan) both represent the yellow color morph and it is therefore necessary to apply a new name to the white morph. Given the chromosomal heterogeneity of the white morph and the inevitability of future taxonomic changes, the following description and type citations are based exclusively upon 64-spored, sexually reproducing populations occurring in Baja California.

Notholaena californica D. Eaton subsp. **leucophylla** Windham, subsp. nov.—TYPE: MEXICO. Baja California: low granitic hills 4 mi N of Rancho Mesquital, 30 Mar 1961, *Wiggins 16187* (holotype: US!; isotypes: DS! MICH! RSA!).

A subsp. *californica* lamina abaxialiter farina albida (non flavida) obtecta, sporangiis 64 sporas capientibus, sporis vulgo minoribus minus quam (x) = 55 μm longis metientibus differt.

Plants epipetric. Rhizomes compact to short-creeping, usually branched, the branches 3–7 mm in diameter; rhizome scales linear-subulate, weakly bicolorous with a broad, dark brown central stripe and very narrow, poorly defined pale brown margins; scale margins ciliate-denticulate. Leaves 4–15 × 1.5–6 cm. Petioles brown, often longer than blade, rounded adaxially, bearing scattered farinose glands and a few scales near base. Blades broadly pentagonal, 3-pinnate proximally, usually slightly longer than wide; abaxial surface with conspicuous white farina; adaxial surface distinctly glandular. Basal pinnae much larger than adjacent pair, strongly inequilateral, the proximal basiscopic pinnules greatly enlarged. Ultimate segments sessile to subsessile, narrowly adnate to costae or occasionally free; segment margins recurved but rarely concealing mature sporangia. Sporangia containing 64 spores. Spores averaging 44–54 μm long.

Distribution. Mexico, Baja California; rocky slopes and cliffs, usually on granitic or volcanic substrates; 100–1100 m.

PARATYPES. **Mexico.** BAJA CALIFORNIA SUR: 2–3 km inland from Bahia Candelero, Isla Espíritu Santo, *Wiggins 16129* (DS, MEXU, MICH, UT).

Gastony and Windham (1989) reported that *Notholaena grayi* Davenp. comprised two cytotypes, a sexual diploid with $n = 30$ chromosomes and an apogamous triploid showing $n = 90$. The two cytotypes are recognizable morphologically because of differences in spore number per sporangium and spore size. Sexual diploid populations produce 32 spores per sporangium, and the spores are relatively small, averaging 44–54 μm long. Apogamous triploid collections (including the type of *N. grayi*) yield 16 (or 8) spores per sporangium and, though the spores are quite variable in size, all samples average more than 55 μm long. Isozyme studies indicate that the apogomous triploid cytotype is an autopolyploid derivative of the sexual diploid, and Gastony and Windham (1989) suggested that these cytotypes might best be recognized as varieties. Additional work has revealed ecogeographic distinctions between the cytotypes of *N. grayi*; the sexual diploid occupies habitats in and around the Sonoran Desert, and the apogamous triploid occurs primarily in the Chihuahuan Desert. The discovery of a strong geographic component to variation in *N. grayi* argues for subspecific recognition of the taxa involved. The previously undescribed sexual diploid cytotype is characterized as follows.

Notholaena grayi Davenp. subsp. **sonorensis** Windham, subsp. nov.—TYPE: MEXICO. Sonora: steep sides of canyon at La Mina Verde, 31 km W of Cumpas, 3600 ft, 23 Sep 1934, *Wiggins 7400* (holotype: US!; isotypes: ARIZ! DS! MICH! UC!).

A subsp. *grayi* sporangiis 32 sporas capientibus, sporis minus quam (x) = 55 μm longis metientibus, chromosomatum numero $n = 30$ differt.

Plants epipetric. Rhizomes compact to short-creeping, usually branched, the branches 3–7 mm in diameter; rhizome scales linear-subulate, uniformly blackish brown or weakly bicolorous with very narrow, poorly defined pale brown margins; scale margins ciliate-denticulate. Leaves 5–25 × 1.5–4 cm. Petioles brown, shorter than or equal to blade, rounded adaxially, glandular-farinose, bearing scattered hairs and scales. Blades linear-lanceolate, 2-pinnate-pinnatifid proximally, 3–6 times longer than wide; abaxial surface with conspicuous whitish farina throughout and lanceolate, entire scales scattered along rachises and costae; adaxial surface distinctly glandular. Basal pinnae equal to or slightly larger than adjacent pair, more or less equilateral, the proximal basiscopic pinnules not greatly enlarged. Ultimate segments sessile, broadly adnate to costae; segment margins slightly recurved, rarely concealing mature sporangia. Sporangia containing 32 spores. Spores averaging 44–54 μm long. Chromosome number: $n = 30$ (from paratypes indicated by *).

Distribution. U.S.A., southern Arizona, and western Mexico south to Jalisco; rocky slopes and cliffs, usually on granitic or volcanic substrates; 1200–2000 m.

PARATYPES. **U.S.A.** ARIZONA: Cochise Co., Mule Mountains, Box Canyon Ranch, lower end of Box Canyon, *Yatskievych 84-195* (ARIZ, UT); northeast slope of the Huachuca Mts along unnamed tributary of Soldier Creek, *Windham (784) & Yatskievych** (ASC, KANU, NY); Pima Co., Baboquivari Mts, Baboquivari Canyon, *Gould & Haskell 3228* (ARIZ, MO); Santa Cruz Co., W side of Alamo Canyon, Pajarito Mts, *Windham & Yatskievych 225** (ASU, RSA, UT).

PELLAEA

Recent morphological (Windham, unpubl.) and isozyme studies (Gastony 1988) of *Pellaea atropurpurea* (L.) Link and its allies have revealed the existence of apogamous tetraploid hybrids between this species (an apogamous triploid) and diploids within the *P. glabella* Mett. ex Kuhn complex. As a result of their apogamous life cycle, these *P. atropurpurea* × *glabella* s.l. hybrids are reproductively competent and range far beyond the limited areas of parental sympatry. In terms of morphology, the hybrids are most similar to *P. atropurpurea*, which contributed three of the four chromosome sets found in somatic cells of the plants (Gastony 1988). The hybrids are easily distinguished from *P. atropurpurea*, however, by having rachises that are sparsely villous (not densely curly-pubescent) on the adaxial surface, pinnules that are usually less than 30 mm long, and spores averaging more than 62 μm long. As an independently reproducing interspecific hybrid, this taxon cannot be included within any previously recognized species of *Pellaea* and is described here as a new nothospecies. It is named in honor of Gerald J. Gastony, Indiana University, in recognition of his contributions to our understanding of evolutionary patterns in many fern genera, especially *Pellaea*.

Pellaea gastonyi Windham, sp. nov.—TYPE: CANADA. British Columbia: Kinbasket Mountain by Kinbasket River, NW of Golden, 17 Aug 1953, *Calder & Savile 11976* (holotype: US!; isotypes: DAO! UBC! WTU!). Fig. 2.

Pellaeae atropurpureae (L.) Link similis, a qua differt rhachidibus sparsim villosis adaxialiter (non dense crispato-pubescentibus), pinnulis vulgo minus quam 30 mm longis, sporis plus quam (x) = 62 μm longis metientibus; a *P. lyngholmii* Windham pinnis basalibus pinnulis 3–7, nonnullis pinnulis rhachillis longissimis longioribus, frondibus fertilibus plerumque minus quam 6 cm latis differt.

Plants epipetric. Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, uniformly reddish brown or tan, with entire to denticulate margins. Leaves 8–25 × 3–6 cm, slightly dimorphic with sterile leaves shorter than fertile leaves; croziers villous. Petioles reddish purple to dark brown, rounded adaxially, without prominent articulation lines. Blades elongate-deltate to lanceolate, 2-pinnate proximally; rachis straight, rounded adaxially, sparsely villous with long, divergent hairs. Pinnae ascending or perpendicular to rachis, not decurrent on rachis or obscurely so, usually with 3–7 ultimate segments; costae 2–30 mm, usually shorter than ultimate segments. Ultimate segments oblong-lanceolate, 7–30 mm, with obtuse to slightly mucronate apex, sparsely villous along midrib abaxially; segment margins usually recurved on fertile segments, covering less than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 32 spores. Spores averaging 64–72 μm long.

Distribution. Sporadically in western Canada (Alberta, British Columbia, and Saskatchewan) and the central U.S.A. (South Dakota, Wyoming and Missouri); calcareous cliffs and ledges, usually on limestone; 100–1500 m.

PARATYPES. **Canada.** ALBERTA: 6.5 km ESE of Canmore on S side of Grotto Mtn, *Brunton 1289* (CAN, UT).—BRITISH COLUMBIA: east shore of Columbia Lake, *Taylor & Ferguson 3932* (DAO).—SASKATCHEWAN: Cluff Lake area, 58° 21'N, 109° 42'W, *Polson & Hudson 3680B* (DAO, SASK); vicinity of the base of Cornwall Bay, Lake Athabaska, *Raup 6558* (CAN, CAS, US). **U.S.A.** SOUTH DAKOTA: Pennington Co., 6 mi. E of Sheridan Lake, *Stevens 7133* (KANU).—WYOMING: along Moskee Rd 9.6 mi SE of junction of Moskee Rd and I-90, *Gastony 83-68* (IND, UT).

The taxonomic status and evolutionary relationships of taxa constituting the *Pellaea glabella* Mett. ex Kuhn complex have been the source of much debate. In her monograph of *Pellaea* section *Pellaea*, A. Tryon (1957) recognized three varieties of *P. glabella*: an eastern North American apogamous tetraploid (var. *glabella*), a western North American apogamous tetraploid (var. *simplex*), and a western sexual diploid (var. *occidentalis*). An eastern sexual diploid was subsequently discovered by Wagner et al. (1965) but did not receive a formal name (var. *missouriensis*) until 1988.

In the next continent-wide overview of the *P. glabella* complex, Lellinger (1985) treated each of A. Tryon's varieties as a distinct species and relegated the eastern diploid to the status of a minor variant within *P. glabella*. Using primarily isozyme data, Gastony (1988) proposed yet another approach to the taxonomy of this group. Gastony presented evidence that the eastern tetraploid arose as an autopolyploid derivative of the eastern diploid, and that the western tetraploid originated in like manner from the western diploid. Consequently, Gastony (1988) recognized two species in the complex: the eastern North American *P. glabella* (with two varieties) and the western North American *P. occidentalis* (E. Nels.) Rydb. (with two subspecies). In a more recent paper, Gastony et al. (1992) present chloroplast DNA data that appear to support the taxonomic realignments proposed in 1988.

The focal point of controversy in the taxonomic treatment of the *P. glabella* complex relates to the degree of genetic divergence among the various taxa involved. In terms of morphology, many of the key characters used by proponents of

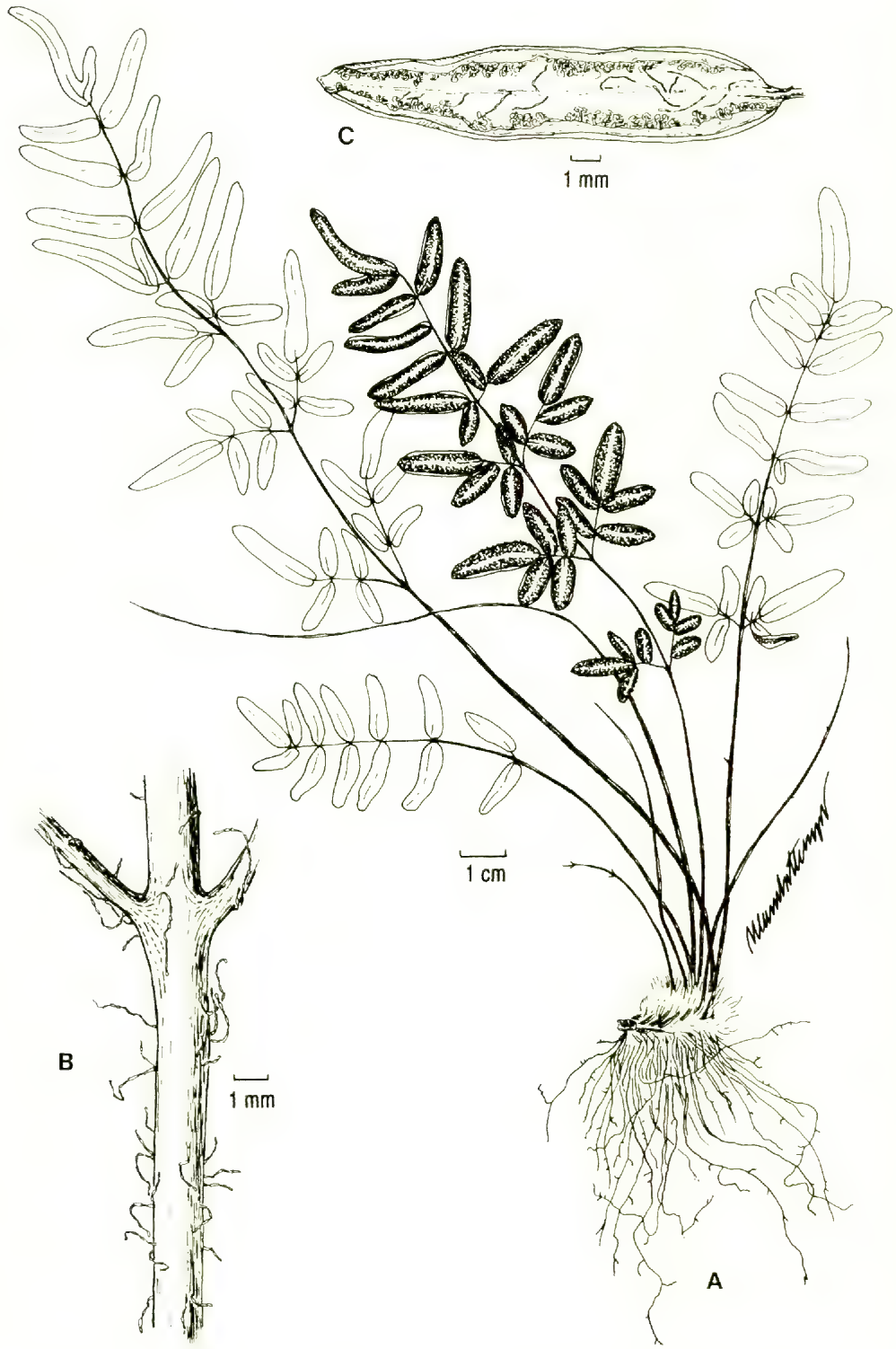

FIG. 2. *Pellaea gastonyi*. A. Habit; note that most costae are shorter than the ultimate segments. B. Adaxial view of portion of rachis; note sparsely villous surface and ascending, obscurely decurrent costae. C. Abaxial view of ultimate segment; note sparsely villous midrib. (Based on *Calder & Savile 11976*.)

multi-species taxonomies (e.g., Butters 1921; Lellinger 1985) fail singly or in combination. Especially prone to overlap are features of the leaf blade, including size, shape, and degree of dissection. These are strongly influenced by habitat, and heavy dependence on them has resulted in frequent misidentification. Because of the subtle morphological differentiation among taxa, the three-species taxonomy has proven largely unworkable on a continent-wide basis.

The same criticism, however, can be leveled at the two-species taxonomy proposed by Gastony (1988). The only morphological characters that consistently distinguish members of the *P. glabella* complex are spore size, spore number per sporangium, petiole color, and the presence or absence of hairs along pinnule midribs. The first three characters separate taxa *within* Gastony's species, so only the fourth (in combination with geography) can be used to differentiate *between* species. This suggests that *P. occidentalis* and *P. glabella* have not diverged sufficiently to be considered separate species, an interpretation supported both by isozymes (Gastony 1988; Windham, unpubl.) and cp DNA studies (Gastony et al. 1992). Isozyme surveys of section *Pellaea* indicate that *P. occidentalis* and *P. glabella* are less divergent genetically than any other pair of *Pellaea* species in North America. In terms of cp DNA, the maximum patristic distance between *P. occidentalis* and *P. glabella* is 11, which is less than 25% of the estimated distance between the *P. glabella* complex and its sister taxon, *P. atropurpurea*. All of these observations argue against the recognition of *P. occidentalis* and *P. glabella* as distinct species.

One further consideration involves the impact of Gastony's (1988) two-species taxonomy on the treatment of the newly recognized nothospecies *P. gastonyi* (*P. atropurpurea* × *glabella* s.l.). If *P. occidentalis* and *P. glabella* are considered separate species, then independently derived populations of *P. gastonyi* in eastern and western North America must also be treated as distinct, because they would represent hybrids between different parental species. The characters that distinguish *P. occidentalis* and *P. glabella* are so subtle that they are completely obscured in hybrids with *P. atropurpurea*, and eastern and western populations of *P. gastonyi* appear to be morphologically indistinguishable. Considering these facts, a more conservative treatment of the *P. glabella* complex seems warranted, and the four taxa will be treated as subspecies of *P. glabella* in *Flora of North America*. This necessitates the following nomenclatural changes.

Pellaea glabella Mett. ex Kuhn subsp. **missouriensis** (Gastony) Windham, stat. nov. *Pellaea glabella* var. *missouriensis* Gastony, Amer. Fern J. 78: 64. 1988.—TYPE: U.S.A. Missouri: Jefferson Co., river bluffs 10 mi W of DeSoto, near jct. of rd H and Big River, *Gastony 83-34-47* (holotype: IND; isotypes: GH, MICH, MO!).

Pellaea glabella Mett. ex Kuhn subsp. **occidentalis** (E. Nelson) Windham, comb. et stat. nov. *Pellaea atropurpurea* var. *occidentalis* E. Nelson, Fern Bull. 7: 30. 1899.—TYPE: U.S.A. Wyoming: Laramie Hills, 13 Jun 1896, *Nelson 1919* (holotype: RM!; isotypes: BRY! MO, NY!).

A series of distinctive *Pellaea* populations discovered in central Arizona by M. D. Windham and D. Lyngholm have proven to consist of apogamous tetraploid hybrids between *P. atropurpurea* and *P. truncata* Goodding (Gastony & Yatskievych 1992). As is the case with *P. gastonyi* (described above), these hybrids are reproductively competent and most similar to the apogamous triploid parent, *P. atropurpurea*, which contributed three of the four chromosome sets found in

somatic cells of the plants (Gastony & Yatskievych 1992). The hybrids are easily distinguished from *P. atropurpurea*, however, by having rachises that are sparsely villous (not densely curly-pubescent) on the adaxial surface, mucronate pinnules that are smaller (usually less than 25 mm long) and more numerous, and spores averaging more than 62 µm long. As an independently reproducing interspecific hybrid, this taxon cannot be included within any previously recognized species of *Pellaea* and is described here as a new nothospecies. It is named in honor of Donavon Lyngholm, codiscoverer of this unusual fern, whose tireless efforts in support of wilderness conservation have helped to ensure the continued survival of this and many other rare species.

Pellaea lyngholmii Windham, sp. nov.—TYPE: U.S.A. Arizona: Yavapai Co., SW side of Fay Canyon ca. 1.39 km SSE of the summit of Bear Mountain, 4775 ft, 23 Sep 1990, *Windham (90-420) & Lyngholm* (holotype: UT!; isotypes: ASU! UC! US!). Fig. 3.

Pellaeae atropurpureae (L.) Link similis, a qua differt rhachidibus sparsim villosis adaxialiter (non dense crispato-pubescentibus), pinnulis vulgo minus quam 25 mm longis, sporis plus quam (x) = 62 µm longis metientibus; a *P. gastonyi* Windham pinnis basalibus pinnulis 7–15, pinnulis rhachillis longissimus persaepe brevioribus, frondibus fertilibus plerumque plus quam 6 cm latis differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear to subulate, 0.1–0.3 mm wide, uniformly brown or tan, with entire to denticulate margins. Leaves 10–30 × 5–15 cm, slightly dimorphic with sterile leaves shorter and less divided than fertile leaves; croziers villous. Petioles dark brown to reddish purple, rounded adaxially, without prominent articulation lines. Blades elongate-deltate to ovate, 2-pinnate proximally; rachis straight, often slightly flattened adaxially, sparsely villous with long, divergent hairs. Pinnae perpendicular to rachis or slightly ascending, not decurrent on rachis, the largest with 7–15 ultimate segments; costae 25–80 mm, usually longer than ultimate segments. Ultimate segments oblong-lanceolate, 10–25 mm, with slightly mucronate apex, sparsely villous abaxially along midrib; segment margins usually recurved on fertile segments, covering less than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 32 spores. Spores averaging 64–72 µm long.

Distribution. U.S.A., central Arizona; rocky slopes and ledges in thin, sandy soil associated with sandstone outcrops; 1200–1800 m.

PARATYPES. **U.S.A.** ARIZONA: Coconino Co., bottom of Damfino Canyon, *Windham (901) & Windham* (UT); Yavapai Co., along small tributary of Dry Creek on NW slope of Capitol Butte, *Windham (721) & Lyngholm* (ARIZ, MO, NMC, UNM, UT); near head of ravine on S side of Fay Canyon, *Windham 7* (ASC).

Pellaea mucronata (D. Eaton) D. Eaton encompasses two morphological extremes that tend to occupy different habitats. The typical 3-pinnate form is scattered throughout California and southern Nevada, usually below 1800 m elevation. The 2-pinnate form with ascending, overlapping pinnae is apparently confined to the Sierra Nevada and Transverse Ranges of California at elevations greater than 1800 m. The taxonomic status of these entities remains in dispute, and they are often treated as mere ecological forms. Wagner et al. (1983) indicated that natural hybrids formed between *P. bridgesii* and these two taxa are morphologically distinct, which suggests that the differences observed between these morphotypes of *P. mucronata* are genetically based. Because they represent well-characterized

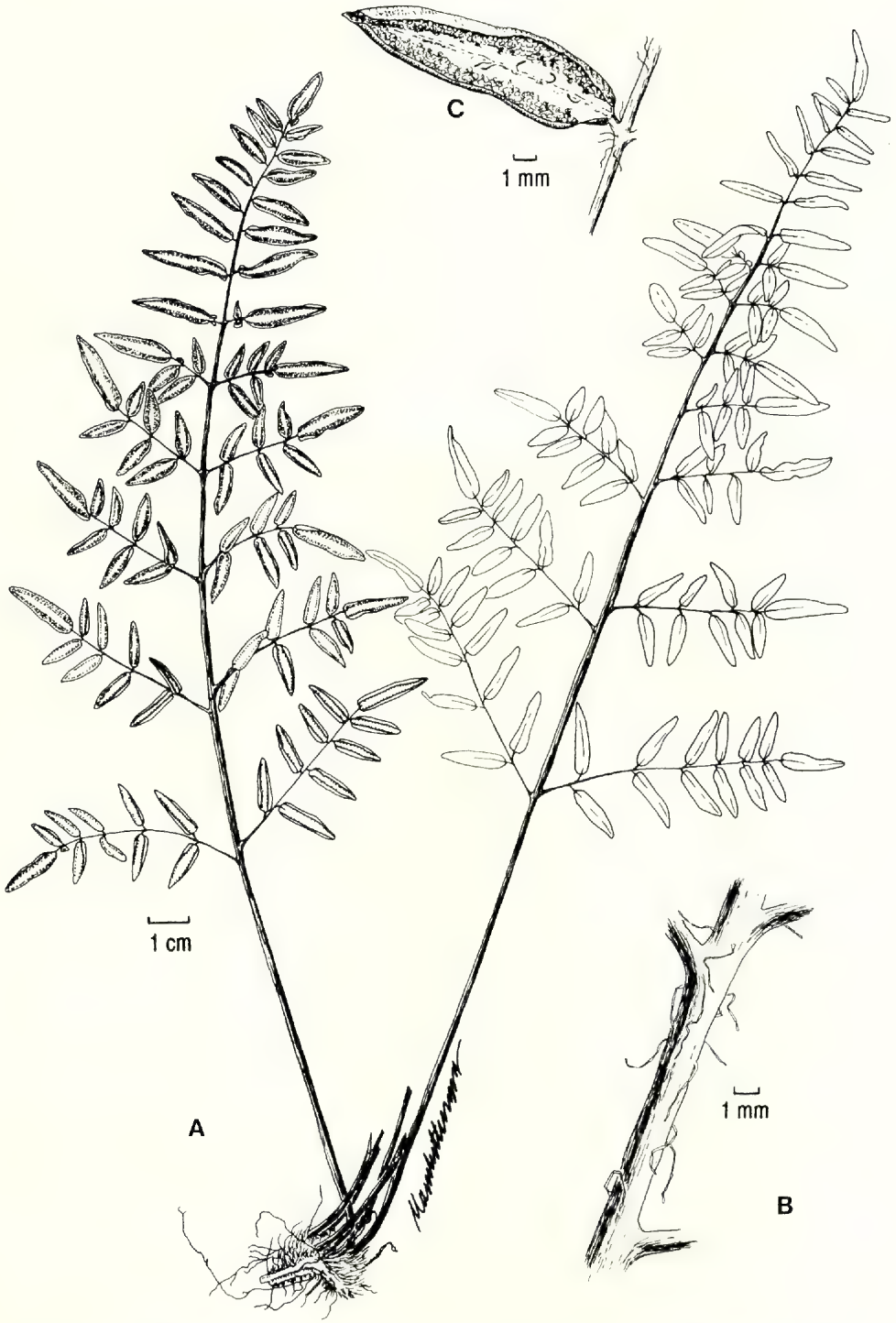

FIG. 3. *Pellaea lyngholmii*. A. Habit; note that most costae are longer than the ultimate segments. B. Adaxial view of portion of rachis; note sparsely villous surface. C. Abaxial view of ultimate segment; note sparsely villous midrib and slightly mucronate apex. (Based on *Windham (90-420) & Lyngholm.*)

genetic variants that tend to occupy discrete ranges, they will be treated as subspecies in *Flora of North America*, and the following nomenclatural change is necessary.

Pellaea mucronata (D. Eaton) D. Eaton subsp. **californica** (Lemmon) Windham, comb. et stat. nov. *Pellaea wrightiana* var. *californica* Lemmon, Ferns Pacific Coast, 10. 1882.—TYPE: U.S.A. California: San Bernardino Mts, 30 May 1876, *Lemmon* (lectotype, designated by A. Tryon, 1957: UC!; isolectotypes: F, GH, US).

As defined by A. Tryon (1957), *Pellaea ternifolia* (Cav.) Link included two varieties: a widespread taxon with ternately dissected pinnae (var. *ternifolia*) and a primarily North American element in which the pinnae are fully pinnate (var. *wrightiana*). Even with the recognition of var. *wrightiana* as a distinct species (following Wagner 1965), *P. ternifolia* remains a highly variable taxon. Within the area covered by *Flora of North America*, there are three genetically distinct taxa characterized by differences in leaf morphology and chromosome number. A population in west Texas consisting of glabrous-leaved diploids with short (< 18 mm) ultimate segments and grooved or flattened petioles appears to represent the typical form of the species (judging from the original description and a photo of the holotype at UT). The most common form occurring in the flora is a glabrous-leaved tetraploid with long (> 18 mm) ultimate segments and more or less terete petioles. The third taxon, a pubescent-leaved tetraploid mentioned by A. Tryon (1972), is apparently very rare in the flora but commonly encountered in Mexico. Isozyme and chromosome studies suggest that both tetraploids are segmental allopolyploids produced by hybridization between typical *P. ternifolia* and other (as yet unidentified) diploid elements within the *P. ternifolia* complex. The two tetraploid taxa have not received formal recognition in the past and are here described as subspecies.

Pellaea ternifolia (Cav.) Link subsp. **arizonica** Windham, subsp. nov.—TYPE: U.S.A. Arizona: Cochise Co., SW slopes of the Dragoon Mountains ca. 1.59 km NNE of Granite Spring, 6050 ft, 18 Mar 1981, *Windham 246* (holotype: UT!; isotypes: ASC! ASU! MO! UC! US!).

Subsp. *ternifoliae* similis a qua differt numero majore pinnarum indivisarum ad apicem frondium, nonnullis pinnulis plus quam 18 mm longis, stipitibus adaxialiter convexis vel leviter complanatis distaliter, sporis plus quam (x) = 46 μm longis metientibus, chromosomatum numero $n = 58$; a subsp. *villosa* Windham pinnis omnino glabris, rhachidibus glabrescentibus pilis paucis perdispersis differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, strongly bicolorous, with a sharply defined, black central stripe and brown, erose-dentate margins. Leaves 10–50 × 3.5–8 cm, monomorphic; croziers sparsely villous to glabrescent. Petioles black or dark purple, rounded or slightly flattened adaxially in distal portion, without prominent articulation lines. Blades linear-lanceolate to ovate, deeply pinnate-pinnatifid proximally; rachis straight, often flattened adaxially, glabrous or with a few widely scattered hairs. Pinnae perpendicular to rachis or slightly ascending, not decurrent on rachis, ternately divided in proximal portion of blade; costae absent. Ultimate segments linear-oblong, 18–40 mm, with a mucronate apex, glabrous throughout; segment margins recurved on fertile segments, rarely covering more than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 64 spores. Spores averaging 46–53 μm long. Chromosome number: $n = 58$ (from holotype population and paratypes indicated by *).

Distribution. U.S.A., southeastern Arizona and Trans-Pecos Texas, and northern Mexico, Chihuahua and Sonora; cliffs and rocky slopes on a variety of acidic substrates including quartzite and granite; 1700–2400 m.

PARATYPES. **U.S.A.** ARIZONA: Cochise Co., Ramsey Canyon, Huachuca Mts, *Peebles, Harrison & Kearney 3501* (ARIZ); southeast wall of Huachuca Canyon, *Windham 303** (ASC, CAS, KANU, TEX, UNM, UT); Santa Cruz Co., Madera Canyon, Santa Rita Mts, *Phillips 3000* (ARIZ, US).—TEXAS: Brewster Co., Big Bend National Park, Chisos Mountain Basin Area, canyon along south rim of the Basin, *Tryon & Tryon 5042* (MEXU, UT).

Pellaea ternifolia (Cav.) Link subsp. **villosa** Windham, subsp. nov.—TYPE: MEXICO. Hidalgo: rocky hills, Lena Station, 8300 ft, 24 Aug 1905, *Pringle 10025* (holotype: LL!; isotypes: ARIZ! BRY! CAS! COLO! DAO! ENCB! F! GH! IND! KANU! LL! MSC! OKLA! SMU! TEX! UC! US! VT! WIS!).

Subsp. *ternifoliae* et subsp. *arizonicae* Windham similis, a quibus differt pinnis pilis dispersis secus venas principales abaxialiter, rhachidibus villosis apprime axillis pinnarum; insuper differt a subsp. *ternifolia* numero majore pinnarum indivisarum ad apicem, pinnulis plus quam 18 mm longis, stipitibus adaxialiter convexis vel leviter complanatis distaliter, sporis plus quam (x) = 46 μm longis metientibus, chromosomatum numero $n = 58$.

Plants epipetric (rarely terrestrial). Rhizomes compact, 5–10 mm in diameter; rhizome scales linear-subulate, 0.1–0.3 mm wide, strongly bicolorous, with a black central stripe and brown, erose-dentate margins. Leaves 10–50 × 3–7 cm, monomorphic; croziers densely villous. Petioles black or dark purple, rounded or slightly flattened adaxially in distal portion, without prominent articulation lines. Blades linear-lanceolate, deeply pinnate-pinnatifid proximally; rachis straight, often flattened or slightly grooved adaxially, villous throughout or with hairs concentrated in axils of pinnae. Pinnae ascending or rarely perpendicular to rachis, not decurrent on rachis, ternately divided in proximal portion of blade; costae usually absent. Ultimate segments linear-oblong, 18–40 mm, with a mucronate apex, sparsely villous abaxially along midribs; segment margins usually recurved on fertile segments, often covering more than 1/2 the abaxial surface. Sporangia long-stalked, not intermixed with glandular paraphyses, containing 64 spores. Spores averaging 46–53 μm long. Chromosome number: $n = 58$ (from paratypes indicated by *).

Distribution. Central and northern Mexico from Puebla north to Durango, Chihuahua and Coahuila, one disjunct locality in the Davis Mountains of west Texas, U.S.A.; rocky slopes and ledges on various (mostly calcareous) substrates; 1800–2700 m.

PARATYPES. **Mexico.** DURANGO: near km post 14 on Hwy 40 W of Ciudad Durango, *Ranker (829b) & Yatskievych** (UT).—PUEBLA: Mpio. de Felipe los Angeles, La Candelaria, *Ventura A. 4289** (MICH).—SAN LUIS POTOSÍ: Sierra San Miguelito, 15 mi W of San Luis Potosí, *Rollins & Tryon 58218** (GH).

Pleopeltis

A recent paper by Mickel and Beitel (1987) detailing the extent of hybridization between *Pleopeltis* and *Polypodium* raises questions concerning the circumscription of these genera. The authors recognize five different hybrid taxa, which they assign to the intermediate genus ×*Pleopodium*. In each case, the *Polypodium*

species involved in the hybridization event belonged to subgenus *Marginaria*, the scaly polypodies. It is important to note that typical members of *Polypodium* (subg. *Polypodium*) are not known to hybridize with either *Pleopeltis* or any species of subg. *Marginaria*.

Pleopeltis and the scaly polypodies have long been considered close allies (de la Sota 1966, 1973; Pichi Sermolli 1977; Tryon & Tryon 1982), and they share a number of distinctive morphological traits. Unlike most members of the Polypodiaceae s.s., both *Pleopeltis* and the scaly polypodies have scales scattered over the abaxial surface of the blade. These laminar scales are of a distinctive type (stalked, peltate, and centrally clathrate) otherwise unknown in the Polypodiaceae (Baayen & Hennipman 1987). Another unusual characteristic shared by these groups is the tendency for developing sori to be protected by a "false indusium" composed of overlapping, peltate scales. The discovery of laminar nectaries in both *Pleopeltis* (Windham, unpubl.) and *Polypodium* subg. *Marginaria* (Koptur et al. 1982) provides yet another feature that separates these taxa from most other Polypodiaceae. Similarities in spores, rhizome scales, and venation patterns round out the list of characters suggesting a close evolutionary relationship between these two groups.

The features that distinguish the scaly polypodies from *Pleopeltis* are quite apparent, even to the untrained eye. Leaf blades of the polypodies are deeply pinnatifid, whereas those of *Pleopeltis* are usually simple and entire. There are several exceptions to this rule, however, most notably *Pleopeltis angusta* (the type species of the genus) and *Pleopeltis fallax* (a species recently transferred from *Polypodium* by Mickel and Beitel). The primary character used to separate the two groups involves the attachment of the soral scales, which arise directly from the receptacle in *Pleopeltis* but are peripheral to the sorus in *Polypodium* subg. *Marginaria*. Another distinction frequently mentioned in the literature (Wagner & Wagner 1975; Tryon & Tryon 1982) involves venation patterns in the leaf. Laminar venation patterns tend to be more complex in *Pleopeltis*, and each sorus is served by several veins that form a complex reticulum within the receptacle (Wagner & Wagner 1975). The scaly polypodies, on the other hand, have simpler vascular systems (with fewer anastomoses) and each sorus is supplied by a single vein.

Although the characters that distinguish *Pleopeltis* from the scaly polypodies are conspicuous, their value for generic segregation must be reexamined in light of the hybridization data (Wagner & Wagner 1975). The association of each sorus with several veins in *Pleopeltis* suggests that they may be coenosori, compound structures formed by the fusion of several individual sori (see Wagner 1986). Support for this hypothesis derives from the occurrence of small "islands" of parenchyma within the vascular reticulum of the receptacle, a situation observed in many coenosoral taxa including the closely related *Marginariopsis* (Wagner 1986). If the "sori" of *Pleopeltis* are actually coenosori, then the distinctive receptacular scales could have originated as peripheral scales that became incorporated into the coenosori during soral fusion. This idea finds support in the work of Baayen and Hennipman (1987), who report that the "paraphyses" (receptacular scales) of *Pleopeltis* are unique among polypodioid ferns in being structurally identical to the laminar scales distributed around the sori. These observations suggest that both the complex venation patterns and the receptacular scales of *Pleopeltis* may have arisen through soral fusion. Such fusion could, in turn, be a direct result of blade simplification (the evolution of a simple blade from a pin-

natifid ancestral form). Thus, the three features that distinguish *Pleopeltis* from the scaly polypodies could be viewed as a complex of covarying traits, all of which may trace their origin to a simple change in blade dissection. If this interpretation is correct, it casts serious doubt on the generic separation of *Pleopeltis* and *Polypodium* subg. *Marginaria*.

The foregoing discussion of *Pleopeltis* and *Polypodium* raises an important question concerning the classification of polypodioid ferns: Are the scaly polypodies more closely related to *Polypodium* (as the current classification suggests) or to *Pleopeltis*? This question has been addressed through isozyme and cpDNA analyses (Andrews, Haufler, & Windham, unpubl.) of a small set of species representing each of the three lineages. Although some enzyme loci were too variable to be useful, the most conservative enzymes (such as TPI) indicated that *Pleopeltis* and the scaly polypodies form a cohesive group quite distinct from both temperate and tropical members of subg. *Polypodium*. Similar results were obtained from a preliminary cpDNA analysis, which indicated that *Pleopeltis* and the scaly polypodies were nearly identical to one another but well differentiated from subg. *Polypodium*. Thus, the molecular analyses strongly support the hypothesis that the scaly polypodies are more closely related to *Pleopeltis* than they are to other species of *Polypodium*.

A combination of morphological, molecular, and hybridization data suggests that the classification of this group of polypodioid ferns is in need of revision. As currently defined, *Pleopeltis* appears to be paraphyletic, whereas *Polypodium* is clearly polyphyletic. This problem can be resolved by either submerging *Pleopeltis* into a broadly defined *Polypodium* or redefining *Pleopeltis* to include the scaly polypodies.

The first option would require fewer nomenclatural changes, because most species of *Pleopeltis* have, at one time or another, resided within *Polypodium*; however, this approach substantially increases the heterogeneity of *Polypodium*, which is already large and poorly defined. The inclusion of *Pleopeltis* within *Polypodium* would weaken the case for recognizing other segregate genera, such as *Campyloneurum*, *Microgramma*, and *Phlebodium*, and would result in making *Polypodium* even more heterogeneous. This approach would also reduce the information content of the classification system, because it does not reflect either the close relationship between *Pleopeltis* and the scaly polypodies or their substantial evolutionary divergence from *Polypodium* subg. *Polypodium*.

The second option (redefining *Pleopeltis* to include the scaly polypodies) requires a greater number of nomenclatural changes and increases the heterogeneity of *Pleopeltis*, which can no longer be identified solely by the presence of receptacular scales. When circumscribed to include the scaly polypodies, *Pleopeltis* can still be recognized by a combination of apparent synapomorphies, including the unique laminar scales, the presence (in immature sori) of a "false indusium" composed of overlapping, peltate scales, and the presence of nectaries near the base of the blade. The transfer of the scaly polypodies to *Pleopeltis* makes that genus a natural (probably monophyletic) group and improves prospects for clarifying the definition and phylogenetic relationships of *Polypodium*. The resulting classification also provides a more accurate representation of evolutionary relationships, emphasizing both the clear phylogenetic affinity between *Pleopeltis* and the scaly polypodies and their genetic isolation from *Polypodium* subg. *Polypodium*.

Redefining *Pleopeltis* to include the scaly polypodies seems the best approach to the taxonomic problems outlined above, and that is the course adopted here.

Unresolved problems of synonymy and species boundaries within the scaly polypodies prevent the wholesale transfer of all 40+ species at this time. Until studies of this group are completed, I propose to transfer only those species to *Pleopeltis* that hybridize with species currently included in *Pleopeltis* and occur within (or immediately adjacent to) the region covered by *Flora of North America*.

Pleopeltis guttata (Maxon) E. G. Andrews & Windham, comb. nov. *Polypodium guttatum* Maxon, Contr. U.S. Natl. Herb. 17: 575. 1916.—TYPE: MEXICO. Coahuila: near Saltillo, 15–30 Apr 1898, *Palmer 65* (holotype: US).

Pleopeltis polypodioides (L.) E. G. Andrews & Windham, comb. nov. *Acrostichum polypodioides* L., Sp. pl. 2: 1068. 1753.—TYPE: JAMAICA, collector unknown (lectotype, designated by Weatherby, 1939: Herb. Plukenet, BM).

Pleopeltis polypodioides (L.) E. G. Andrews & Windham var. **acicularis** (Weatherby) E. G. Andrews & Windham, comb. nov. *Polypodium polypodioides* (L.) Watt var. *aciculare* Weatherby, Contr. Gray Herb. 124: 33. 1939.—TYPE: COSTA RICA. San Francisco de Guadalupe, *Tonduz 8476* (holotype: GH; isotype: NY).

Pleopeltis polypodioides (L.) E. G. Andrews & Windham var. **michauxiana** (Weatherby) E. G. Andrews & Windham, comb. nov. *Polypodium polypodioides* (L.) Watt var. *michauxianum* Weatherby, Contr. Gray Herb. 124: 31. 1939.—TYPE: U.S.A. Virginia: Nansemond Co., Kilby, *Fernald, Long & Fogg 4703* (holotype: GH).

Pleopeltis thyssanolepis (A. Braun ex Klotzsch) E. G. Andrews & Windham, comb. nov. *Polypodium thyssanolepis* A. Braun ex Klotzsch, Linnaea 20: 392. 1847. SYNTYPES: COLOMBIA. *Moritz 22* (B; isosyntype: P), *Otto 896* (B; isosyntype: P).

A northern variant of *Pleopeltis thyssanolepis* described by Wendt (1980) as var. *riograndense* appears to represent a distinct species. It differs from typical representatives of *P. thyssanolepis* in having sparsely scaly petioles and leaves, petiole scales that are mostly ovate or lance-ovate (not suborbicular), mostly free venation with < 40% of the sori within areoles, and basal blade segments that are distinctly alternate. These morphological differences, combined with a tetraploid chromosome number, suggest that this taxon may have originated as a hybrid between *P. thyssanolepis* and *P. guttata*. Recognition as a distinct species within *Pleopeltis* requires the following nomenclatural change.

Pleopeltis riograndensis (Wendt) E. G. Andrews & Windham, comb. et stat. nov. *Polypodium thyssanolepis* A. Braun ex Klotzsch var. *riograndense* Wendt, Amer. Fern J. 70: 6. 1980.—TYPE: U.S.A. Texas: Presidio Co., lower Indian Cave Canyon (side canyon of Dead Horse Canyon), N side of Chinati Mts, 16 Oct 1977, *Butterwick & Lott 3897* (holotype: TEX; isotypes: GH, MEXU).

Polypodium

Collections of *Polypodium* from the southern Rocky Mountains traditionally have been assigned to a single taxon, variously known as *P. hesperium* Maxon or *P. vulgare* L. var. *columbianum* Gilbert. Martens (1943), Lang (1969), and Windham (1985), however, reported that some specimens from the region have paraphyses (= sporangiasters) scattered among the sporangia. Such sporangiasters are absent from the sori of *P. hesperium* (Lang 1969, 1971), and southern Rocky Mountain collections exhibiting them have been identified as *P. virginianum* L. (Martens 1943), *P. montense* Lang (Lang 1969), or *P. amorphum* Suksdorf (Windham 1985).

As noted by Martens (1943), collections of *Polypodium* with sporangiasters from the southern Rocky Mountains are rather similar to the eastern North American taxon known as *P. virginianum*. The western plants differ from typical representatives of *P. virginianum* in having narrower leaf blades (mostly < 3.5 cm wide) and sporangiasters with fewer glandular trichomes. The Rocky Mountain taxon also shows a strong resemblance to *P. amorphum*, a Pacific Northwest species formerly known as *P. montense*. Plants from the southern Rocky Mountains differ from this species in having sporangiasters with fewer glandular trichomes, strongly tuberculate spores averaging more than 62 μm long, and a chromosome number of $n = 74$.

The discovery that the southern Rocky Mountain taxon was tetraploid led Windham (1985) to hypothesize that it arose as a hybrid between a typical form of *P. amorphum* and a "local (i.e., Rocky Mountain) form with strongly tuberculate spores." Recent isozyme analyses support a modified version of this scenario. These studies clearly indicate that the southern Rocky Mountain taxon is an allotetraploid whose parentage includes *P. amorphum*. The other parent (i.e., the variant of *P. amorphum* with strongly tuberculate spores) is the circumboreal diploid now known as *P. sibiricum* Siplivinskij, which extends south in the Rocky Mountains as far as central British Columbia. The involvement of *P. sibiricum* in the origin of the southern Rocky Mountain taxon also explains its resemblance to *P. virginianum*, which originated as a hybrid between *P. sibiricum* and the eastern North American *P. appalachianum* (Haufler & Windham 1991). As an allotetraploid hybrid between *P. amorphum* and *P. sibiricum*, the southern Rocky Mountain taxon cannot be included within any previously recognized species of *Polypodium* and is described here as a nothospecies.

Polypodium saximontanum Windham, sp. nov.—Type: U.S.A. Colorado: La Plata Co., E side of Vallecito Creek ca. 2.15 km NNE of its confluence with Fall Creek, 8240 ft, 25 Jun 1990, *Windham (90-231) & Windham* (holotype: UT!; isotypes: BRY! COLO! KANU! MO! UC!). Fig. 4.

Polypodii amorphoi Suksdorf simile, a quo differt sporangiasteribus trichomatibus paucioribus, sporis tuberculatis plus quam (x) = 62 μm longis metientibus, chromosomatum numero $n = 74$; a *P. virginiano* L. laminis plerumque minus quam 3.5 cm latis, sporangiasteribus trichomatibus paucioribus differt; a *P. hesperio* Maxon soris sporangiasteribus instructis, paleis rhizomatum atrobrunneis grosse dentatis et contortis distaliter, paleis abaxialibus rhachidum caducis, lanceolato-

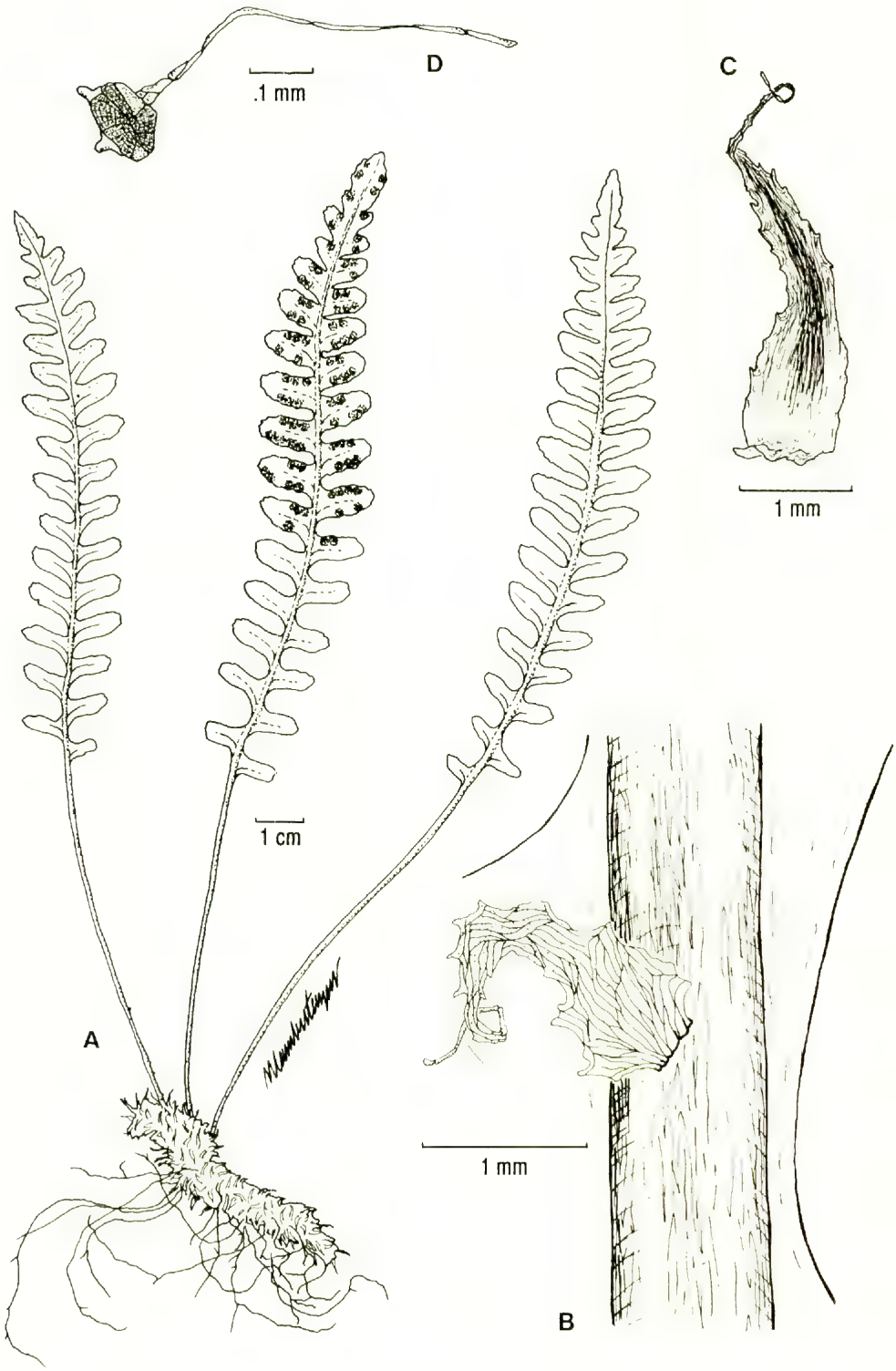

FIG. 4. *Polypodium saximontanum*. A. Habit; note narrow, almost linear leaves and submarginal sori. B. Abaxial view of portion of rachis; note persistent, lanceolate scale. C. Bicolorous rhizome scales with dentate margins and contorted tip. D. Sporangiaster from sorus; note small number of glands on head. (Based on *Windham (90-231) & Windham.*)

ovatis plerumque plus quam 6 cellulis in latitudine; a *P. sibirico* Siplivinskij differt soris sporangiasteribus glandulosis instructis, sporis plus quam (x) = 62 μm longis metientibus, chromosomatum numero $n = 74$.

Plants epipetric. Rhizomes creeping, 2–7 mm in diameter, usually whitish pruinose, acrid-tasting; rhizome scales lanceolate, 20–30 cells wide just above the point of attachment, contorted distally, often coarsely dentate, weakly bicolorous with a dark central region and pale brown margins. Leaves 3–27 × 1–4 cm. Petioles slender, 0.75–1.5 mm in diameter. Blades narrowly oblong to linear, deeply pinnatifid, usually widest near the middle, coriaceous to subcoriaceous, with widely scattered glands on both surfaces; rachis sparsely scaly to glabrescent abaxially, glabrous adaxially; rachis scales lanceolate-ovate, usually more than 6 cells wide. Blade segments oblong, 2–8 mm wide, with rounded (rarely broadly acute) apex and entire to crenulate margins; segment midrib glabrous adaxially; veins free, forking 1–2 times, obscure in mature leaves. Sori circular, usually submarginal, 1–2 mm in diameter. Sporangiasters present, fewer than 40 per sorus, the bulbous heads with 2–6 small glandular hairs (rarely glabrous). Spores averaging 62–70 μm long, conspicuously tuberculate with blunt projections 3–5 μm in height. Chromosome number: $n = 74$ (from the paratypes indicated by *).

Distribution. U.S.A., Colorado, north-central New Mexico, southeastern Wyoming and the Black Hills of South Dakota; cracks and ledges on rock outcrops, apparently confined to granitic and gneissic substrates; 1800–3000 m.

PARATYPES. **U.S.A.** COLORADO: Gunnison Co., small tributary of Spring Creek, *Windham 363** (ASC, UBC); SE side of the Taylor River, *Windham 361** (ARIZ, ASC, UNM), *Windham 364** (ASC, ASU, UTC); W wall of Spring Creek Canyon, *Windham 362** (ASC, UT); Saguache Co., along Cochetopa Creek, *Windham 359** (ASC, COLO).—NEW MEXICO: Rio Arriba Co., vicinity of Brazos Canyon, *Standley & Bollman 10626, 11195* (US).—WYOMING: Carbon Co., Platte River Canyon, *Dorn 4397, 4398* (RM).

Woodsia

The application of modern biosystematic techniques to the study of North American species of *Woodsia* has revealed a complex web of evolutionary relationships (Windham 1987b) and the existence of several undescribed taxa. The most significant changes involve the *W. mexicana* Fée complex, an extraordinarily heterogeneous assemblage occurring in a wide range of habitats from South Dakota to central Mexico. Reexamination of the type specimens and original descriptions for taxa in the *W. mexicana* complex reveals that *W. mexicana* s.s. is absent from the region covered by *Flora of North America*. Isozyme and chromosome studies of North American collections traditionally identified as *W. mexicana* indicate that they represent three undescribed species here recognized as *W. phillipsii*, *W. neomexicana*, and *W. cochisensis*.

Specimens of *W. phillipsii* have been identified consistently as *W. mexicana* and have been considered typical of that species by many authors (e.g., Brown 1964). Rediscovery of the type specimen of *W. mexicana* (Windisch 1982) and careful examination of Fée's original description reveal the fallacy of this interpretation. *Woodsia phillipsii* differs from *W. mexicana* in having 1) long, completely filamentous indusial segments, 2) a greater number of indusial segments per sorus, 3) multicellular (often filamentous) translucent projections on pinnule margins, 4) glandular hairs with relatively thin stalks, 5) a greater number of

pinnules per pinna, 6) enlarged hydathodes readily visible on the adaxial leaf surface, and 7) smaller spores averaging 37–44 µm long. In addition, plants of *W. mexicana* from eastern Mexico proved to be tetraploids (Windham, unpubl.), whereas chromosome counts derived from *W. phillipsii* are consistently diploid. Isozyme analyses indicate that *W. phillipsii* is the basic diploid of the *W. mexicana* group and was involved, as one parent, in the allopolyploid origins of *W. neomexicana*, *W. cochisensis*, and *W. mexicana*; as such, it should be considered a separate species. It is named in honor of Walter S. Phillips, a pioneer in the study of Arizona ferns, whose collections and ideas have proven invaluable to subsequent researchers.

Woodsia phillipsii Windham, sp. nov.—TYPE: U.S.A. Arizona: Cochise Co., Rucker Canyon, Chiricahua Mts, canyon sides in pine woods, 6500 ft, 7 Oct 1945, *Phillips 2854* (holotype: GH!; isotypes: ARIZ! ASC! UBC! US!). Fig. 5.

Woodsiae mexicanae Fée et *W. neomexicanae* Windham similis, a quibus differt marginibus pinnularum projecturis multicellularibus saepe filamentosis translucentibus e dentibus exorientibus, pinnis plerumque 7–18 paribus segmentorum non imbricatorum, gradatim attenuatis ad apicem anguste acutum, sporis minus quam (x) = 44 µm longis metientibus, chromosomatum numero $n = 38$; insuper a *W. mexicana* Fée differt segmentis indusiorum basi filamentosis, pilis gracilibus ad apicem cellula inconspicue tumida et glandulosa terminatis.

Plants epipetric (rarely terrestrial). Rhizomes compact to short-creeping, the individual branches usually 3–8 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 5–35 × 1.5–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at the base). Blades lanceolate, usually 2-pinnate proximally, sparsely to moderately glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with scattered glandular hairs and narrow scales. Pinnae elongate-deltate to elliptic, longer than wide, often attenuate to a narrowly acute apex, the largest divided into 7–18 pairs of distinct, well-separated pinnules; abaxial and adaxial surfaces somewhat glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins somewhat thickened, often lustrous adaxially, sparsely glandular, appearing ciliate due to the presence of multicellular translucent projections on teeth that are often prolonged to form twisted filaments; vein tips usually enlarged to form whitish hydathodes visible adaxially. Indusia of narrow, filamentous segments, these uniseriate for most of their length, often greatly surpassing mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 37–44 µm long. Chromosome number: $n = 38$ (from the paratypes indicated by *).

Distribution. U.S.A., southern Arizona, southern New Mexico, and Trans-Pecos Texas, and northern Mexico, Chihuahua and Sonora; cliffs and rocky slopes, usually on quartzite or various igneous substrates; 1600–3200 m.

PARATYPES. **Mexico.** CHIHUAHUA: Mpio. Guachochic, N of Basiguare, *Bye 8039* (COLO); Tecolote 10 mi W of Chinatu, *Correll & Gentry 23006* (LL, MO, US). **U.S.A.** ARIZONA: Cochise Co., SE wall of Huachuca Canyon, *Windham 298** (UT), *Windham 302** (ASC, ASU).—NEW MEXICO: Grant Co., S side of Iron Creek in the Mimbres Mts, *Windham (611) & Haufler* (NMC, UC, UT, UTEP); Hidalgo Co., Animas Mts, upper Indian Creek Canyon, *Wagner 1757* (UNM).—TEXAS: Brewster Co., on trail from Boot Spring to South Rim, *Warnock 1105* (TEX, US).

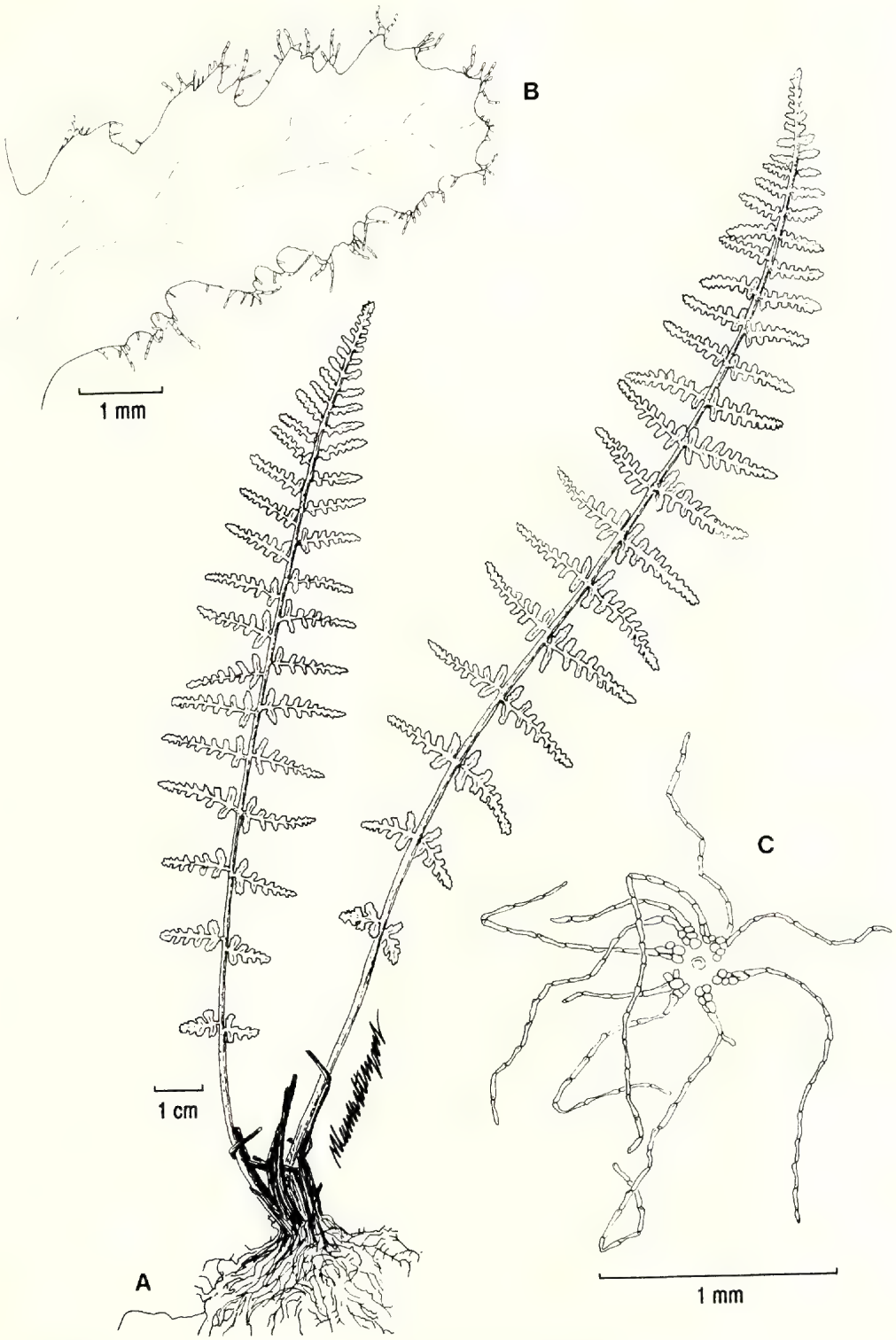

FIG. 5. *Woodsia phillipsii*. A. Habit; note attenuate pinnae divided into numerous, well-separated pinnules. B. Adaxial view of pinnule showing multicellular, filamentous projections on margin. C. Sorus with sporangia removed; note long, filamentous indusial segments. (Based on *Windham (611) & Haufler*.)

Woodsia neomexicana has also been associated with *W. mexicana*, though occasional specimens have been misidentified as *W. oregana*. The latter tendency is not surprising because isozyme data indicate that *W. neomexicana* represents an allotetraploid hybrid between *W. phillipsii* and a diploid member of the *W. oregana* complex. Similarities between *W. neomexicana* and *W. mexicana* probably result from the fact that they share a genome derived from *W. phillipsii*. Nevertheless, *W. neomexicana* differs from *W. mexicana* in having longer, completely filamentous indusial segments, a greater number of indusial segments per sorus, leaf blades that are glabrescent or sparsely glandular, and glandular hairs with relatively thin stalks. Features distinguishing *W. neomexicana* from *W. phillipsii* and *W. oregana* are summarized in the the diagnosis presented below. As a fertile allotetraploid hybrid between the basic diploid member of the *W. mexicana* complex and *W. oregana*, *W. neomexicana* should be recognized as a distinct species, characterized as follows.

Woodsia neomexicana Windham, sp. nov.—TYPE: U.S.A. New Mexico: Socorro Co., along small tributary of Water Canyon in the Magdalena Mts ca. 5.84 km SE of the summit of North Baldy, 7050 ft, 23 Aug 1990, *Windham (90-365) & Rabe* (holotype: UT!; isotypes: ARIZ! ASU! BRY! COLO! GH! MICH! MO! NMC! NY! TEX! UC! UNM! US!). Fig. 6.

Woodsiae mexicanae Fée similis, a qua differt segmentis indusiorum filamentosis e basi, laminis glabrescentibus vel sparsim glandulosis, pilis gracilibus ad apicem cellula inconspicue tumida et glandulosa terminatis; a *W. oregana* D. Eaton differt stipitibus pallide brunneis vel stramineis ubique, filamentis indusiorum sporangia matura excedentibus, marginibus pinnularum projecturis translucentibus e dentibus exorientibus; a *W. phillipsii* Windham differt marginibus pinnularum projecturis translucentibus 1–2-cellularibus (raro multicellularibus) e dentibus, pinnis plerumque segmentis minus quam 7-jugis imbricatis, versus apicem abrupte angustatis apice late rotundatis, sporis plus quam (x) = 44 μm longis metientibus, chromosomatum numero $n = 76$.

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 5–9 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 4–30 × 1.5–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades linear to lanceolate, usually pinnate-pinnatifid proximally, glabrescent to sparsely glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with scattered glandular hairs and rare, hairlike scales. Pinnae ovate-deltate to elliptic, longer than wide, abruptly tapered to a rounded or broadly acute apex, the largest divided into 3–7 pairs of closely spaced pinnules; abaxial and adaxial surfaces glabrescent to sparsely glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins thin, nonlustrous, with widely scattered glands and 1–2-celled translucent projections on most teeth; vein tips occasionally enlarged to form whitish hydathodes visible adaxially. Indusia of narrow filamentous segments, these uniseriate for most of their length, usually surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 44–52 μm long. Chromosome number: $n = 76$ (from the paratypes indicated by *).

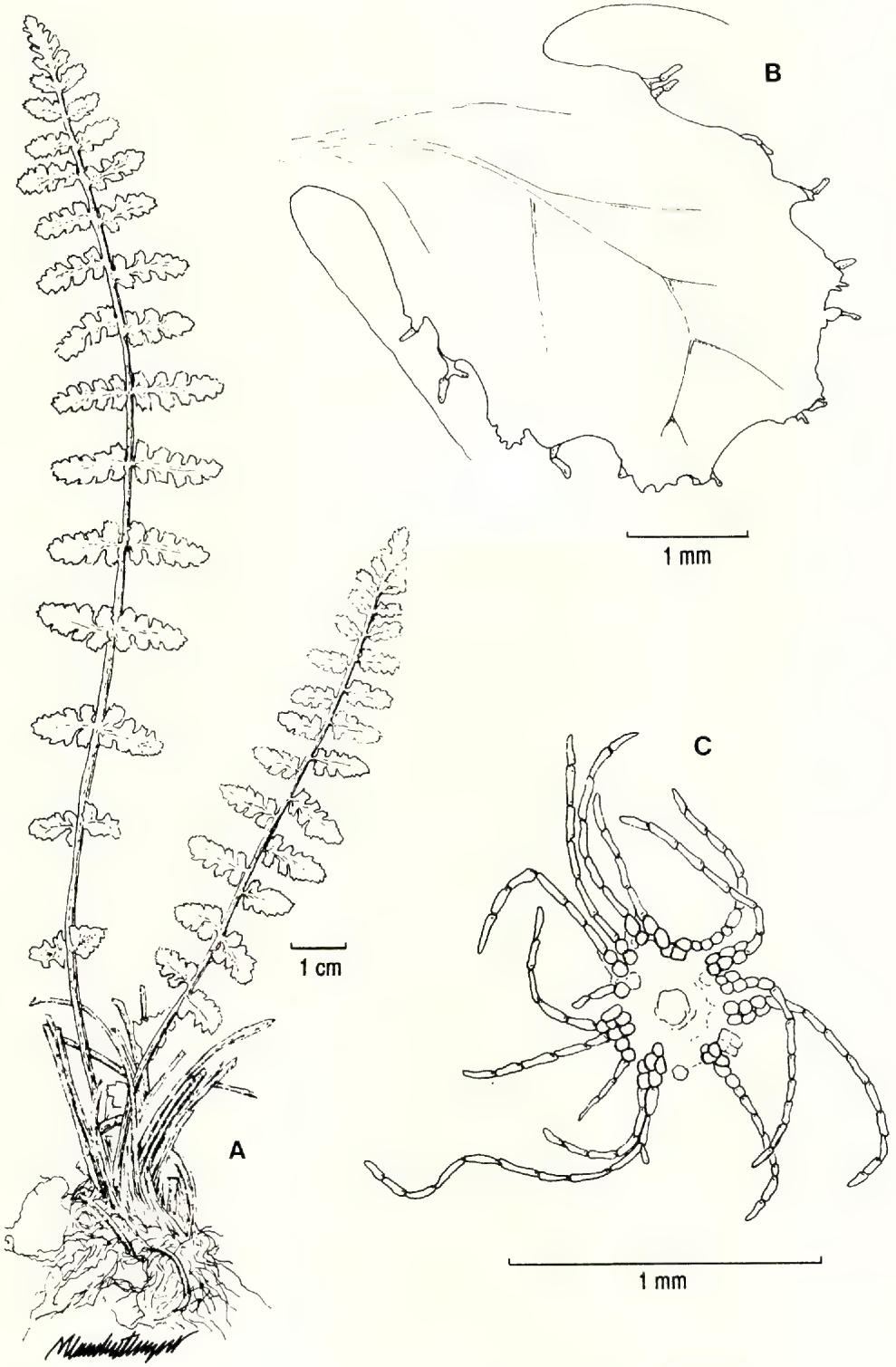

FIG. 6. *Woodsia neomexicana*. A. Habit; note rounded pinna apices and small number of closely spaced pinnules. B. Adaxial view of pinnule showing 1–2-celled projections on margins. C. Sorus with sporangia removed; note long, filamentous indusial segments. (Based in *Windham (90-365) & Rabe.*)

Distribution.U.S.A., New Mexico, Arizona, southern Colorado, western Oklahoma, and Trans-Pecos Texas, one disjunct population in eastern South Dakota; cliffs and rocky slopes, usually on sandstone, quartzite, or various igneous substrates; 300–3500 m.

PARATYPES. **U.S.A.** ARIZONA: Coconino Co., cliffs W of Lenox Park, San Francisco Peaks, *Windham 195** (ARIZ, ASC); Gila Co., below Hi View Point on the Mogollon Rim, *Windham 178* (ASC).—COLORADO: La Plata Co., along trail on W side of Vallecito Creek, *Windham (90-247) & Windham* (COLO, UT, UTC).—NEW MEXICO: Colfax Co., vicinity of Ute Park, *Standley 13832* (US).—OKLAHOMA: Caddo Co., Red Rock Canyon State Park near Hinton, *Lellinger 214* (US).—TEXAS: Jeff Davis Co., across rd from "Point of Rocks" roadside park on scenic drive about 11 mi from Ft. Davis, *Correll 33688* (ENCB, LL, NCU); Presidio Co., North Chinati Mountains, *Warnock 19239* (SRSC).

Specimens of *W. cochisensis* traditionally have been identified as *W. plummerae* Lemmon or (less often) *W. mexicana*. The association with *W. plummerae* stems from the widely held belief that the broad indusial segments and somewhat glandular blade of *W. cochisensis* exclude it from *W. mexicana*. To the contrary, reexamination of the type specimen and original description of *W. mexicana* reveals that these features are characteristic of that species and thus do not serve to distinguish it from either *W. plummerae* or *W. cochisensis*. The three taxa are clearly distinct in other features, however, and worthy of recognition as separate species. *Woodsia cochisensis* differs from *W. plummerae* in having 1) petioles that are light brown or stramineous throughout, 2) leaf blades that are sparsely to moderately glandular and never viscid, 3) glandular hairs with thin stalks and inconspicuously swollen tips, 4) pinnule margins that are usually thickened and lustrous on the adaxial surface, and 5) vein tips enlarged to form hydathodes readily visible on the adaxial surface. It differs from *W. mexicana* in having fewer, narrower glands on the leaf, pinnule margins that are usually thickened and lustrous on the adaxial surface, and well-developed hydathodes readily visible on the adaxial surface. *Woodsia cochisensis* is easily distinguished from other North American members of the *W. mexicana* group (*W. phillipsii* and *W. neomexicana*) by having indusial segments that are broad and non-filamentous for much of their length. Isozyme and chromosome studies suggest that *W. cochisensis* is an allotetraploid that originated through hybridization between *W. phillipsii* and an undescribed Mexican diploid. As such, it should be considered a distinct species characterized as follows.

Woodsia cochisensis Windham, sp. nov.—TYPE: U.S.A. Arizona: Cochise Co., SE wall of Huachuca Canyon in the Huachuca Mts ca. 2.85 km SE of Blacktail Spring, 6000 ft, 31 Aug 1985, *Windham (781) & Yatskievych* (holotype: UT!; isotypes: ARIZ! ASU! MICH! UC! US!). Fig. 7.

Woodsiae plummerae Lemmon similis, a qua differt stipitibus pallide brunneis vel stramineis ubique, laminis sparsim vel moderate glandulosis, haud viscidis, pilis gracilibus ad apicem inconspicue tumidis glandulosis, marginibus pinnularum plerumque incrassatis, adaxialiter nitidis, apicibus venarum dilatatis et formantibus hydathodo albido adaxialiter; a *W. mexicana* Fée differt glandulis paucioribus et angustioribus in lamina, marginibus pinnularum plerumque incrassatis et nitidis adaxialiter, hydathodis manifestis; a *W. phillipsii* Windham et *W. neomexicana* Windham segmentis indusiorum latis non filamentosis praeter apicem differt.

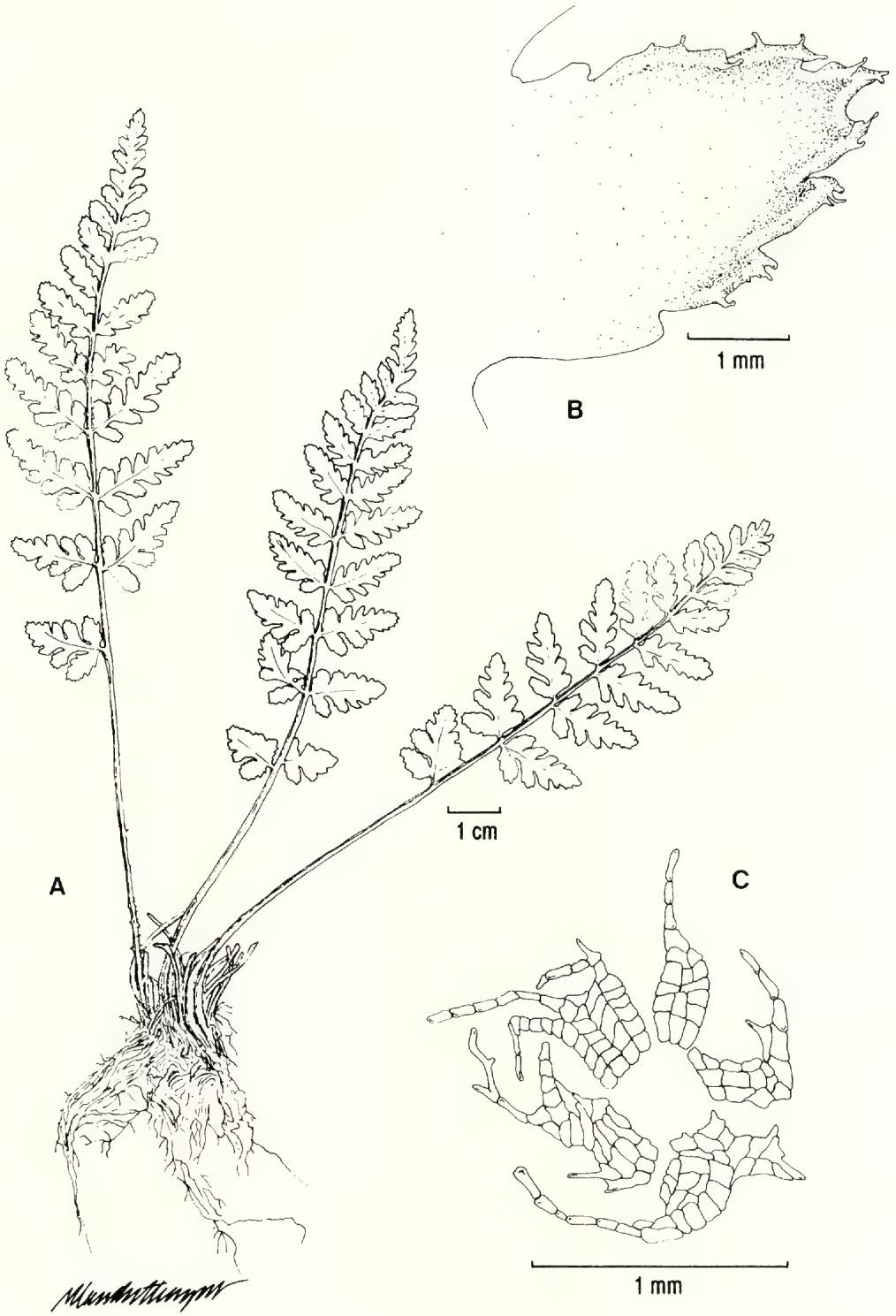

FIG. 7. *Woodsia cochisensis* . A. Habit. B. Adaxial view of pinnule showing thickened margins with scattered glands and 1–2-celled projections. C. Sorus with sporangia removed; note relatively broad indusial segments that are multiseriate proximally but often divided and uniseriate distally. (Based on *Windham (781) & Yatskievych.*)

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 4–9 mm wide, with a few persistent petiole bases of unequal lengths; rhizome scales narrowly lanceolate, often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 5–25 × 1.6–6 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades narrowly lanceolate to ovate, pinnate-pinnatifid to 2-pinnate proximally, sparsely to moderately glandular but never viscid, the glandular hairs with thin stalks and slightly expanded tips; rachises with glandular hairs and occasional narrow scales. Pinnae ovate-deltate to elliptic, longer than wide, abruptly tapered to a rounded or broadly acute apex (rarely attenuate), the largest divided into 4–9 pairs of closely spaced pinnules; abaxial and adaxial surfaces glandular, devoid of eglandular hairs or scales. Pinnules dentate, often shallowly lobed; pinnule margins usually thickened, lustrous adaxially, sparsely glandular, with 1–2-celled translucent projections on some teeth; vein tips enlarged to form whitish hydathodes visible adaxially. Indusia of relatively broad segments, these multiseriate much of their length but usually divided and uniseriate distally, often surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 43–49 μm long. Chromosome number: $n = 76$ (from the holotype population).

Distribution. U.S.A., southern Arizona and southwestern New Mexico, and northern Mexico, Chihuahua and Sonora; shaded ledges and alcoves near springs and seeps, usually on granitic or volcanic substrates; 1000–2200 m.

PARATYPES. **Mexico.** CHIHUAHUA: Barranca de Batopilas between La Bufa and Wimivo, *Bye 6086* (COLO). **U.S.A.** ARIZONA: Cochise Co., unnamed tributary of Stronghold Canyon East, Dragoon Mts, *Windham 309* (ASC); Pima Co., Baboquivari Mts, *Peebles, Harrison & Kearney 3800* (ARIZ, MO); Rincon Mts, *Harrison & Kearney 7977* (ARIZ, US); south wall of Box Canyon, Santa Rita Mts, *Windham 167* (ASC, ASU, KANU); Santa Cruz Co., Sycamore Canyon, *Goodding & Goodding 423* (ARIZ, RM, US); Tumacacori Mts, Rock Corral Spring, *Fletcher 3899* (UNM).

Recent chromosome studies reveal that *Woodsia obtusa* comprises two cytotypes that show evidence of morphologic and ecogeographic differentiation. The tetraploid cytotype is found throughout the eastern United States, commonly occurring on limestone. The diploid cytotype occurs at the western edge of the species range and is usually found on sandstone or granite. The geographically restricted diploid taxon differs from the widespread tetraploid in having leaf blades that are often finely cut and nearly tripinnate, rhizomes that are short- to long-creeping and usually less than 5 mm in diameter, and smaller spores averaging less than 42 μm long. Chromosome and isozyme data suggest that the tetraploid cytotype of *W. obtusa* probably was derived directly from the diploid cytotype through autopolyploidy. Although Sprengel did not designate a type specimen, the original description and the collection locality cited (Pennsylvania) leave little doubt that the type material of *Woodsia obtusa* was tetraploid. It appears that none of the published names in *Woodsia* are applicable to the diploid cytotype of this species, which is here described as a new subspecies.

Woodsia obtusa (Sprengel) Torrey subsp. **occidentalis** Windham, subsp. nov.—TYPE: U.S.A. Texas: Llano Co., W side of Inks Lake, on hillside in granite area, 16 Apr 1945, *Lundell 13484* (holotype: LL!; isotypes: LL! RM!).

A subsp. *obtusa* differt pinnulis proximalibus pinnarum infimarum profunde lobatis vel pinnatifidis, laminis saepe subtiliter incisis fere tripinnatis, rhizomatibus brevi- vel longi-repentibus plerumque minus quam 5 mm diametro, sporis minus quam (x) = 42 μm longis metientibus, chromosomatum numero $n = 38$.

Plants epipetric or occasionally terrestrial. Rhizomes short- to long-creeping, the individual branches usually 3–5 mm wide, with a few persistent petiole bases of unequal length; rhizome scales often uniformly brown but at least some distinctly bicolorous with a dark central stripe and pale brown margins. Leaves 8–40 × 2.5–10 cm. Petioles often somewhat brittle, light brown or straw-colored when mature (occasionally darker at very base). Blades lanceolate to narrowly ovate, usually 2-pinnate-pinnatifid proximally, moderately glandular and rarely somewhat viscid, most of the glandular hairs with thick stalks and distinctly bulbous tips; rachises with glandular hairs and scattered, narrow scales. Pinnae ovate-deltate to elliptic, longer than wide, often attenuate to a narrowly acute apex, the largest divided into 5–14 pairs of distinct, well-separated pinnules; abaxial and adaxial surfaces glandular, devoid of eglandular hairs or scales. Pinnules dentate, the proximal ones usually deeply lobed; pinnule margins thin, nonlustrous, sparsely to moderately glandular, lacking cilia or translucent projections on the teeth; vein tips usually enlarged to form whitish hydathodes visible adaxially. Indusia of relatively broad, nonfilamentous segments, these multiseriate throughout, concealed by or slightly surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 35–42 μm long. Chromosome number: $n = 38$.

Distribution. U.S.A., Oklahoma, central Texas, southeastern Kansas, northeastern Arkansas, and the extreme southwestern corner of Missouri; cliffs and rocky slopes, especially on sandstone and granitic substrates; 200–500 m.

Paratypes. **U.S.A.** Kansas: Woodson Co., T26S, R14E, NE1/4, sec. 14, in sandy soil of a rocky wooded hillside in uplands, *Lathrop 637* (GH, KANU, US).—Oklahoma: Comanche Co., along trail near top of Elk Mtn, Wichita Mountains Wildlife Refuge, *McMurry 1203* (OKL, OKLA); Johnston Co., "Devil's Den" near Tishomingo, *Palmer 39442* (GH, MO, US).—Texas: Burnet Co., Inks Lake State Park, *Hartman 918* (KANU); Granite Mountain, *Palmer 10260* (DS, MO); Gillespie Co., Bear Mountain, *Correll & Correll 12753* (COLO, LL, MICH, SMU, UC).

In his monograph of the genus *Woodsia*, Brown (1964) divided *W. oregana* into two varieties: a diploid (var. *oregana*) thought to span the continent and a tetraploid (var. *cathcartiana*) supposedly restricted to the vicinity of Taylor's Falls on the Minnesota-Wisconsin border. The strong morphological resemblance between these two taxa led Brown to hypothesize that var. *cathcartiana* was an autotetraploid derivative of var. *oregana*. Subsequent chromosome and isozyme work on *W. oregana* has substantially altered our understanding of the distribution and relationships of these taxa. Chromosome surveys of 30 populations scattered across the continent reveal that the tetraploid cytotype of *W. oregana* is actually more common and widespread than the diploid, extending diagonally across North America from California to eastern Canada. Diploid populations, on the other hand, are apparently confined to the Pacific Northwest. The two taxa are nearly allopatric, and isozyme data indicate that var. *cathcartiana* is definitely not an autotetraploid derived from known diploid populations. Although the morphological features that distinguish var. *oregana* and var. *cathcartiana* are subtle, the sharp ecogeographic and genetic discontinuities observed suggest that these taxa should be recognized at a higher taxonomic level. They will be treated as subspecies in *Flora of North America*, which requires the following nomenclatural change.

Woodsia oregana D. Eaton subsp. **cathcartiana** (Robinson) Windham, stat. nov. *Woodsia cathcartiana* B. L. Robinson, Rhodora 10: 30. 1908.—TYPE: U.S.A. Minnesota: Taylor's Falls of the St. Croix River, 1874, *Cathcart s.n.* (holotype: GH!).

In the original description of *Woodsia oregana*, Eaton (1865) mentioned two syntypes: 1) Dalles of the Columbia River, *Major Raines* in 1855, and 2) Montium Scopulosorum sub. lat. 39°–41°, *Hall & Harbour 690a*. Examination of the original specimens in the Eaton Herbarium at Yale University reveals that the first collection represents the Pacific Northwest diploid cytotype of *W. oregana*, whereas the second belongs to the widespread tetraploid taxon here called *W. oregana* subsp. *cathcartiana* (Robins.) Windham. In order to stabilize the nomenclature of *W. oregana* and maintain current application of infraspecific names, the first of the two specimens cited by Eaton is here chosen as the lectotype of the species.

Woodsia oregana D. Eaton, Canad. Naturalist & Quart. J. Sci., n.s. 2: 90. 1865.—TYPE: U.S.A. Oregon: Dalles of the Columbia River, *Major Raines* in 1855 (lectotype, here designated: Y!; isolectotypes: GH, K).

Woodsia scopulina D. Eaton shows substantial variation in leaf size, shape, and dissection, and in the abundance of multicellular hairs on the pinnae. Although much of this variation seems to be environmentally induced, chromosome and isozyme studies have identified three morphogenetic variants worthy of taxonomic recognition. The most distinctive taxon is represented by a series of populations confined to montane habitats in the southeastern United States. Plants found in this region differ from other collections of *W. scopulina* in having 1) narrowly lanceolate rhizome scales that are mostly bicolorous with pale brown margins and a continuous, dark central stripe, 2) broad (non-filamentous) indusial segments, and 3) some blade hairs composed of five or more cells.

Taylor (1947) recognized the distinctive nature of these eastern populations and described them as a new species, *Woodsia appalachiana*. Brown (1964: 98), however, placed this name in synonomy under *W. scopulina*, stating that "the differences are not constant and are so minor that I am not considering even varietal status for this entity." Contrary to Brown's assertion, the differences between the Appalachian taxon and typical representatives of *W. scopulina* from western North America are both stable and significant. The only apparent connection between these two entities consists of scattered populations in the Great Lakes region and western United States that preliminary data suggest may have originated through hybridization. Because of their geographic isolation and morphological distinctiveness, the Appalachian/Ozarkian populations of *W. scopulina* will be treated as a distinct subspecies in *Flora of North America*, which necessitates the following nomenclatural change.

Woodsia scopulina D. Eaton subsp. **appalachiana** (Taylor) Windham, stat. nov. *Woodsia appalachiana* T. M. C. Taylor, Amer. Fern J. 37: 88. 1947.—TYPE: U.S.A. West Virginia: on a mountain 4 mi N of Old Sweet, 14 Sep 1903, *Steele & Steele 306* (holotype: GH!).

As mentioned above, collections of *Woodsia scopulina* from the Great Lakes region tend to bridge the geographic and morphologic gap between subsp. *appa-*

lachiana and subsp. *scopulina*. Preliminary evidence suggests that these plants are tetraploid hybrids genetically isolated from diploid populations of *W. scopulina*. They are most similar to subsp. *scopulina*, from which they differ in having larger spores (averaging > 50 μm long) and some rhizome scales that are weakly bicolorous with clusters of sclerotic cells near the center that form a narrow, usually discontinuous, dark central stripe. The Great Lakes taxon also occurs sporadically in western North America, where it is sympatric with subsp. *scopulina*. Despite regional sympatry, these two taxa are rarely found growing together, suggesting that they differ in ecological tolerances and/or habitat requirements. Although the morphological features that distinguish the Great Lakes taxon are subtle, evidence of strong genetic and ecogeographic isolation suggest that it is worthy of formal taxonomic recognition. None of the names currently available in *Woodsia* are applicable to this taxon, which is here described as a new subspecies.

Woodsia scopulina D. Eaton subsp. **laurentiana** Windham, subsp. nov.—TYPE: CANADA. Quebec: Gaspé Co., Tourelle, on sandstone sea-cliffs, 19–21 Aug 1905, *Collins & Fernald 25351* (holotype: GH!; isotypes: CAN! CAS! GA! GH! MICH! NY! POM! UC! US!).

A subsp. *scopulina* sporis plus quam (x) = 50 μm longis metientibus, paleis rhizomatum interdum infirme bicoloribus prope centrum fuscatis fasciculis angustatis plerumque discontinuis cellularum scleroticarum differt; a subsp. *appalachiana* (Taylor) Windham paleis rhizomatum lanceolato-ovatis infirme (non valde) bicoloribus, pilis raro plus quam 5 cellulis longis in pinnis, segmentis indusiorum angustioribus et saepe filamentosis distaliter, sporis plus quam (x) = 50 μm longis metientibus differt.

Plants epipetric (rarely terrestrial). Rhizomes compact, the individual branches usually 5–10 mm wide, with few to many persistent petiole bases of unequal lengths; rhizome scales ovate-lanceolate, most uniformly brown but at least some with clusters of dark, sclerotic cells near the center forming a narrow, usually discontinuous stripe. Leaves 9–35 × 1–8 cm. Petioles relatively brittle and easily shattered, reddish brown to dark purple proximally when mature. Blades lanceolate to linear-lanceolate, 2-pinnate proximally, moderately glandular and rarely somewhat viscid, the glandular hairs with thick stalks and distinctly bulbous tips; rachises usually with abundant glandular and eglandular hairs. Pinnae lanceolate-deltate to ovate, longer than wide, usually gradually tapered to an acute apex (occasionally attenuate), the largest divided into 5–14 pairs of more or less closely spaced pinnules; abaxial and adaxial surfaces glandular and sparsely villous with long, eglandular hairs concentrated near the midribs. Pinnules dentate, often shallowly lobed; pinnule margins thin, nonlustrous, glandular and sparsely ciliate with long, eglandular hairs; vein tips slightly (if at all) enlarged, barely visible adaxially. Indusia of relatively narrow segments, these multiseriate proximally but often divided into uniseriate filaments distally, concealed by or slightly surpassing the mature sporangia, composed of cells that are more or less isodiametric. Spores averaging 50–57 μm long. Chromosome number: $n = 76$ (in collections from the western U.S.A.).

Distribution. Bimodal distribution with a cluster of populations in the Great Lakes/St. Lawrence region (Ontario, Quebec, and Minnesota) and scattered records in western North America (Alberta and British Columbia south to California and possibly Arizona); cliffs and rocky slopes on a variety of substrates including both granite (acidic) and limestone (basic); 0–3000 m.

PARATYPES. **Canada.** ONTARIO: Nipissing District, Algonquin Provincial Park, ca. 300 yds due E of campsite at N end of Hilliard Lake, *Britton s.n.* (CAN, DAO, OAC, TRT); Thunder Bay District, E side of Cloud Bay, *Garton 18531* (CAN, DAO, LKHD); Laverendrye Provincial Park, E shore of North Fowl Lake, *Brunton 6862* (CAN, OAC, UT).—Quebec: Gaspé Co., Gulf of St. Lawrence, Christie, *Fernald & Pease 24800* (CAN, GH, MICH, NY, US). **U.S.A.** MINNESOTA: Cook Co., face of cliff north of center of East Pike Lake, *Burns & Hendrickson 231* (COLO, MIN, MO, RM); St. Louis Co., near Grand Portage, north shore of Lake Superior, *Wiggins 14945* (DS).

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NEW SPECIES OF HAWAIIAN PTERIDOPHYTES [1]

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The best treatment of the ferns and fern allies of Hawaii is still that of Hillebrand (1888) over a century ago. Except for a few monographic studies and reports on individual species, the knowledge of the lower vascular plants of these islands has lagged behind that of the flowering plants.

Intensive field and herbarium studies of Hawaiian pteridophytes since 1984 have revealed a number of taxa, both orthospecies (presumed divergent or cladistic species), varieties (geographically correlated species divisions), and nothospecies (species produced by hybridization), in addition to numerous new nomenclatural changes. It is planned to embody these in a projected manual of the pteridophytes of Hawaii, including approximately 225 native and naturalized orthospecies, varieties, and nothospecies. The purpose of the present paper is to describe some of the newly recognized taxa. Isotypes will be deposited in the Bishop Museum Herbarium (BISH).

Arachniodes insularis W. H. Wagner, sp. nov.

Arachniodes squamis rhizomatis dense confertis, pallide rufis, usque ad 1.3 × 0.5 cm; frons deltato-ovata, usque ad 1.3 m alta, 3–4 (–5)-pinnata, versus apicem gradatim deminuens; sporae praeter modum grandes, circa 60 (50–70) μm longae.

Leathery, finely dissected terrestrial fern. Rhizome short-creeping, 3–7 × 2–5 cm including stipe bases, scales, and roots. Stem scales narrowing gradually to tip, 0.8–1.3 × 0.2–0.5 mm (at base), rather pale reddish brown. Frond ovate-deltate, 0.3–1.3 × 0.1–0.6 m including stipe. Stipe 35–75 cm, with sparse, light-brown scales, but densely scaly in lowest 3–20 cm. Blade 3–4 (–5)-pinnate, the branching anadromous, i.e., the basal acroscopic segments of the pinnae and pinnules appearing first along the axes. Frond tip formed by steady reduction in symmetry. Basiscopic pinnules of lowest pinnae ca. 2× the length of the acroscopic pinnules. Rachis and costae bearing few scattered narrow fibrils 2–3 (–4) cm long. Pinnules elongate-dentate 2–3 (–4) pinnate, the medial ones 10–20 × 3–7 cm. Lamina texture coriaceous. Segment and lobe tips slightly aristate. Color dark shiny green above, slightly paler below. Venation free. Sori round, 0.8–1.2 mm diameter. Indusium leathery, reniform. Spores unusually large, ca. 60 (50–70) mm long. Chromosome number: $n = 82$.

Holotype: E. Maui, SW side of Makawao Forest Reserve along Olinda Pipeline Road. Common in dense woods on rocky stream banks. 6 July 1947. *Wagner 5185* (MICH).

[1] This study is dedicated to Mr. Edwin Bonsey. He was born in Olmsted Falls, Ohio, in 1885, and died in Hilo, Hawaii, in 1978. He was a long time teacher of science in Wailuku, Maui, and his home in Makawao, Maui, was a center for visiting botanical researchers for many years. Without his help, many botanical projects would have been impaired. His knowledge of the flora and the habitats of Haleakala was unmatched, and his commemoration in the naming of Bonsey's Holly Fern is not only merited, but is a token of the gratitude of many botanists.

Other collections: HAWAII: E slope of Mauna Loa. Woods, near Kulani, ±1400 m. 28 June 1915. *Forbes 978-H* (MICH, 2 sheets).—OAHU: Punahou, 800 m. May 1910. *Faurie 362* (MICH).—W. MAUI: Hanaula. Area near reservoir. Frequent along trail. 25 March 1987. *Wagner 87115 et al.* (MICH).

The holotype (Fig. 1) is a rather small-fronded individual but was selected for its excellent rhizome showing the characteristic scales. The plant is generally rare, and found at high altitudes in wet forest, and seems to be most common on Maui. *Arachniodes insularis* has no immediate relatives in the Hawaiian Islands. Concentrated in the mountains of warm parts of central and eastern Asia, the genus is widely distributed but poorly known; it is discussed by Kramer (1990). The main distinguishing marks of the new species (formerly identified with such names as *Rumohra carvifolia* (Kunze) Ching, *Polystichum carvifolium* (Kunze) C. Chr., or *Aspidium aristatum* Sw.) are as follows: Rhizome scales large (up to 1.3 × 0.5 cm) and rather pale reddish brown; ovate deltate fronds up to well over 1 m tall, 3–4 (–5) pinnate, and gradually reduced to the tip; and the unusually large spores (50–70 μm).

Asplenium hobdyi W. H. Wagner, sp. nov.

Species *A. normali* similis sed rachidi supra aliquot proliferationibus instructa; pinnae oblongae, 5–12 mm longae, apice plerumque truncato, auricula basili mediocriter evoluta, margine antico 3–5 prominentiis humilibus instructo.

Tufted ferns of dark damp forest. Rhizome up to 1.5 × 1.0 cm including stipe bases. Stem scales 1.0–1.4 × 0.2–0.4 mm, inconspicuous or invisible, buried among stipe bases and roots, black, triangular. Fertile fronds 10–40 × 0.5–2.0 cm. Blade linear, 1-pinnate. Stipes clustered, up to 12 per plant, glabrous at maturity except at extreme base. Pinnae oblong, 0.5–1.2 × 0.4–0.6 cm, blunt-tipped, dimidiate, the anterior basal auricle absent or poorly developed, shallow and rounded. Margins coarsely and shallowly crenate, not or only slightly overlapping rachis. Texture rather leathery. Veins rather conspicuous, up to 6 on anterior side of pinna, only 1 or 2 on basal side nearly parallel to costa. Rachis proliferations up to 6 per frond proximal from nonproliferous tip. Sori 2.5–3.5 mm long, mostly on the 2–5 veins on the distal side of the pinna, 0–2 on the lower side. Indusium somewhat leathery and conspicuous. Chromosome number: $n = 72$.

HOLOTYPE: E. Maui, Waikamoi, near Olinda Pipeline Trail. Abundant at mouth of dark, wet, rock cave. 27 March 1987. *Wagner 87164* (MICH).

Other collections: MOLOKAI: Head of Waikola Valley, Hanalilolilo. Mossy wet wall of sinkhole on side of ridge. 1200 m. 21 Dec 1932. *St. John 12379 et al.* (BISH).—MAUI: Ahapuaa of Kalialinui, between Puu o Kakae and Puu Nianiau, in closed *Metrosideros*-dominated mesic forest, along upper boundary of Makawao Forest Reserve. Growing in gulch in shade with *Athyrium*. 1967 m. June 1975. *P. Higashino 714* (2 sheets, HAW); Eastern end of Haleakala Crater in upper Kaupo Gap. Growing in shaded gulch of aa lava. With *Styphelia*, *Vaccinium*, *Coprosma*, *Dodonaea*, *Metrosideros*, etc. Infrequent. 16 June 1969. *J. Hendrickson & Richard Vogl* (BISH); NW slope of Puu Kukui, Nahalalua. 28 July 1938. *L. M. Cranwell & C. Skottsberg 2713* (BISH).—HAWAII: Kau District. Kilauea Forest Reserve, 1 mi W of Kulani Cone. NW corner of IBP Study Site. On fallen logs. 1650 m. 18 Jan 1971. *Lamoureux 4429* (HAW). Slope of Mauna Kea, in wet forest. 1500–1800 m. Jan. 1958. *J. F. Rock & T. Lindsay 12* (BISH). Along Saddle Road, 19 mi from Hilo. In dark rainy kipuka. 29 Aug. 1949. *O. Degener et al.* (BISH).

This species exists in dark, moist woods, probably on all of the five largest islands. It is much less common than *Asplenium normale* Don, which usually grows in drier more exposed sites and with which it has traditionally been confused. The following key will separate them.

FIG. 1. *Arachniodes insularis* W. H. Wagner. E. Maui, Makawao Forest Reserve; *Wagner 5185* (MICH).

Proliferations solitary at the aborted tip of the frond, protected by a single infolded pinna. Pinnae 10–22 mm long, elongate, triangular, with more or less rounded pointed tips and well-developed pointed anterior basal auricle; anterior margin shallowly or strongly dentate, with 6–12 marginal projections. Sori with delicate thin indusia. Chromosome number: n = ca. 144. *A. normale.*

Proliferations 1–5 scattered along the upper rachis, not protected by infolded pinnae. Pinnae 5–12 mm long, oblong, with mostly truncate tip and no or poorly developed rounded anterior basal auricle; anterior margins shallowly crenate, with 3–5 marginal projections. Sori with prominent thick indusia. Chromosome number: $n = 72$. *A. hobdyi.*

Cheilanthes takeuchii W. H. Wagner, sp. nov.

C. decipienti similis sed lamina elliptica; rachis plerumque exalata, quam costa basalis 1.9–2.6plo longior, parte prima quam secunda 1.9–3.1plo longiore; pinnae plerumque brevistipitatae vel sessiles; sori paene vel omnino circum apices segmentorum extensi.

Small tufted terrestrial fern. Rhizome compact 0.3–1.4 × 0.3–0.8 cm including 5–25 stipe bases plus root bases. Scales 2.5–3.5 × 0.4–0.7 mm at base, becoming very narrow in upper 1/3 to 2/3, cells at base thin, pale brown, those in narrowed upper part with a central strip of dense, occluded, black cells. Frond elliptic-deltate to elliptic, 10–25 × 3–8 cm including stipe. Rachis wiry, 2.1 (1.9–2.6)× the length of the basal costa, dark maroon to blackish, non-winged in lower sector, the lowest rachis sector 2.7 (1.9–3.1)× as long as the next sector. Blades pinnate to bipinnate. Pinnae mostly opposite, sessile to short-stalked. Pinnules and segments 2–8 mm wide, ovate to linear, approximately parallel-sided, or only slightly tapering to tip. Lamina thick chartaceous, pale green. Marginal coenosori with false indusia running to or stopping just short of tip.

Holotype: Oahu. Diamond Head, open slopes near tunnel, 100–120 m. 22 March 1988. *W. Takeuchi 3824* (MICH).

Other collections: Same locality. Jan. 1988. *Takeuchi & Pyle 1200* (MICH); plants completely dried and brown. 5 June 1991. *Wagner 91009* (MICH).

This curious plant is known only from Diamond Head Crater where it apparently grows only during the winter, the fronds drying up through spring and fall. Its frond outline (Fig. 2) is more like typical species of *Cheilanthes* than the sister species in Hawaii, *C. decora* (Brack.) Tryon & Tryon and *C. decipiens* (Smith) W. H. Wagner. The new species is most likely to be confused with the latter.

Blades sub-triangular, the rachis length 1.5 (1.3– 1.6)× the basal costa length, almost completely pinnatisect, the pinnae mostly adnate; rachis mainly winged, the first sector 1 (0.7–1.3)× as long as the second; most sori running to 0.5–2 (–4) mm of segment tips. *C. decipiens.*

Blade elliptic-deltate to elliptic, the rachis length 2.1 (1.9–2.6)× the basal costa length, 1–2-pinnate, the pinnae mostly short-stalked or sessile; rachis mainly non-winged except distally, the first sector 2.7 (1.9–3.1)× as long as the second; most sori running completely or very close (0.1–0.2 mm) to the segment tips. *C. takeuchii.*

Diellia pallida W. H. Wagner, sp. nov.

A *D. falcata* basi stipitis sparsim squamosa differt, squamis 3–5 × 0.7–1.7 mm, brunneis vel griseis, sine cellulis nigris occlusis; frons quam stipes 3–5plo longior; pinnae basales deltatae et vix redactae.

Small or medium-sized fern of dry, rocky soils with 2–5 upright fronds. Rhizome nearly erect, straight, 1.5–4.0 × 2.0 cm including 3–4 stipe bases plus several dead rachises. Scales brown, gray, or blackish, the cells rarely occluded in central

FIG. 2. *Cheilanthes takeuchii* W. H. Wagner. Oahu, Diamond Head; *Wagner 91001* (MICH). Silhouettes of leaves showing variation. All fronds soriferous except the left. Bar = 5 cm.

area, 3.0–5.0 × 0.7–1.7 mm. Fronds oblong-lanceolate, 20–60 × 5–12 cm. Stipes and rachises brown to pale tan, the surface dull, the surface cells thin-walled. Stipes 10–18 × 0.1–0.3 cm, with very few scales at base. Pinnae simple and straight margined or somewhat undulate or laciniate in luxuriant fronds. Blade tip formed by a simple terminal pinna. Venation strongly anastomosing in the disk, with 2–3 layers of areoles in the basal half of pinnae. Sori variable, commonly more or less fused into coenosori, 0.5–20 mm long, marginal to nearly medial.

HOLOTYPE: Kauai. Mahanaloa Valley, *Wagner 5805* (MICH).

Other collections: KAUAI: Koaie Stream, Waimea Canyon. 3 June 1972. *L. E. Bishop 1305* (HAW); 5 July 1987. *J. Lau 3100* (BISH).

Recent studies have confirmed that *Diellia laciniata* (Hillebr.) Diels is actually a variant of *D. erecta* Brack. The most distinctive feature of *D. pallida* as compared with *D. laciniata* is the light color of the rachis, the palest of all the species. This was confirmed by a study of specimens grown in a greenhouse at the University of California Berkeley, during the years 1950–1952, a voucher specimen of which is deposited in the Harvard Herbaria. The specimen shows that even in greenhouse cultivation, the rachises remain pale because of the absence of black, occluded surface cells. The type of *D. laciniata,* "Ida's Fern, *Lindsaya falcata* var. Knudsen 89 (B)" has black, shiny rachises. Isotypes recently found in storage at the Bishop

Museum show the same condition. In addition, one of the fronds from "Ida's Fern" is entirely non-laciniate and corresponds to typical *D. erecta* except for a greater than usual tendency toward coenosoral fusion. Accordingly we have named as a new species the Kauai plant that is analogous to *D. falcata* of Oahu.

Because no individuals were observed in the single area known for this species (Mahanaloa and Paaiki Valleys, western Kauai, *Wagner 3495, 5805*) since their discovery in the later 1940's, it was assumed that it had become extinct. However, in 1987, Lau discovered a new area for it in Koaie stream valley on the eastern side of Waimea Canyon, at an elevation of 600 m, some nine kilometers to the east of the original locality. A few plants were found on a steep slope in bare soil at the base of a tree in a mixed mesic forest slope with little ground cover. Associated plants included *Acacia koa, Antidesma, Alectryon, Lantana, Melia,* and *Rauwolfia.* Some gametophytes with tiny sporophytes were also seen adjacent to a mature plant. Later, an unidentified specimen (*L. E. Bishop 1305*) from presumably the same locality was located in the University of Hawaii Herbarium.

The closest relative of *D. pallida* is the much more widespread and common *D. falcata* Brack. of Oahu. The following key will separate them.

Stipe base very scaly, the scales 3.0–7.0 × 1.5–3.0 mm, black with occluded cells; thin-walled scales common to abundant on upper stipe and rachis; stipe usually 1/8–1/6 of total frond length; basal pinnae round and usually much reduced; sori mostly separate and borne on short marginal proliferations. *D. falcata.*

Stipe base sparsely scaly, the scales 3.0–5.0 × 0.7–1.7 mm, mainly brown to gray, with no or rarely a few occluded cells in the central area; thin-walled scales sparse or absent on upper stipe and rachis; stipe usually 1/5–1/3 of total frond length; basal pinnae deltate and only a little shorter than those above; sori frequently fused along a line or situated medially below shallow sinuses. *D. pallida.*

Dryopteris tenebrosa W. H. Wagner, sp. nov.

D. glabram minutam simulans sed squamis rhizomatis inconspicuis, 2–5 × 0.3–0.6 mm; frons fertilis oblongo-lanceolata, 5–12 × 0.7–4.0 cm; pinnae lineari-oblongae vel lineari-lanceolatae, usque ad 2.5 × 1.3 cm; segmenta ultima 0.5–1.4 mm lata.

Minute tufted lacy fern of steep dark mossy banks. Rhizome upright, up to 2.0 × 0.8 cm. Stem scales up to 4.0 × 0.4 mm, inconspicuous or invisible, buried among leaf bases and roots, triangular, castaneous, shiny. Fertile fronds 3.0–12.0 × 0.7–4.0 cm. Blades linear-lanceolate to oblong-lanceolate, 1–2- (–3)-pinnate. Stipes extremely narrow, 0.3–2.0 cm long, densely clustered, up to 35 per plant, including remains of previous year's, essentially glabrous, except for a few scattered deciduous scales on teneral fronds. Rachis with wing 0.2–0.3 mm thick. Pinnae linear-oblong to linear-lanceolate, up to 2.5 × 1.3 cm, simple to lobed or pinnate, ultimate lobes or segments if present up to 0.5 × 1.4 mm. Texture thin-coriaceous. Sori borne on fronds as small as 3.0 × 0.7 cm, nearly marginal on acutely pointed lobes. Chromosome number: $n = 41$.

Holotype: Kauai: NaPali-Kona Forest, Kilohana Trail. Kauaikoi Stream. 1200 m. 18 August 1947. *Wagner 5574* (MICH).

Other collection: Type locality. 9 April 1987. *Wagner 87186,* 2 sheets (MICH).

The description is based on 20 plants from a single locality (Fig. 3). This tiny *Dryopteris* grows in colonies near water in deep shade on rocky stream banks,

FIG. 3. *Dryopteris tenebrosa* W. H. Wagner. Kauai, NaPali-Kona Forest; *Wagner 87186* (MICH). Bar = 5 cm.

associated with *Sadleria squarrosa* (Gaud.) Maxon, *Callistopteris* sp., and small plants of *Dryopteris glabra* (Brack.) Kuntze to which the new species is no doubt related. *Dicranopteris linearis* (Burm.) Underw. forms a canopy at the top of the bank. The population has been observed for over four decades.

The new species is contrasted with its nearest relative in the following key:

Stem scales inconspicuous, mostly buried below leaf bases, 2.0–4.0 × 0.2–0.4 mm; fertile fronds linear-lanceolate to oblong-lanceolate, 3.0–12.0 × 0.7–4.0 cm; rachis 0.2–0.3 mm wide; pinnae linear-oblong to linear-lanceolate, up to 2.5 × 1.3 cm; ultimate segments 0.5 × 1.4 mm; texture thin-coriaceous. *D. tenebrosa.*

Stem scales conspicuous, exposed above leaf bases, 8.0–10.0 × 0.3–0.6 mm, fertile fronds triangular-lanceolate, 10–30 × 4–12 cm; rachis 0.4–1.2 mm wide; pinnae up to 5.5 × 3.5 cm; ultimate segments 4.9 × 2.3 mm wide; texture chartaceous.
D. glabra (deep shade form of steep, mossy banks).

The rather similar plant named *Dryopteris parvula* Robinson (1912, p. 593, pl. 44) is described as having "both surfaces of blades and stipes covered with globular glands." Its status is still unknown.

Dryopteris subbipinnata W. H. Wagner & R. W. Hobdy, sp. nov.

D. wallichianam simulans sed pinnis plerumque imbricatis; segmenta proximalia basi humiliter vel profunde lobata, apice rotundata; fasciculus venarum in quoque segmento distaliter 4–5-partitus.

Coarse leathery scaly terrestrial fern. Rhizome up to 35 × 20 cm including old stipe bases; stem apex covered with dense masses of linear scales highly variable in size, 1.0–2.0 × 0.1–0.2 mm (at base), central cells glossy black, lateral cells orange-brown to chestnut-brown. Fronds up to 1.3 × 0.4 m including stipe. Stipes up to 35 cm, the scales like those of stem but smaller and narrower, 3.0– 8.0 × 0.5–1.0 mm. Blades pinnatisect above, pinnate below; tip formed by gradual reduction; blade base somewhat narrowed with several lower pairs of pinnae 2/3 (–1/2) the length of those above. Rachis densely covered with narrow scales like those of

upper stipe. Pinnae in lower 1/2 to 1/3 of blade shallowly to deeply (up to 1/2) cut; segments of adjacent pinnae 15–25 × 5–10 mm, shallowly to deeply lobed, usually overlapping in middle and lower part of blade. Segments of lower part of blade contracted at base or stalked. Costae finely scaly, the scales very narrow 0.2–0.5 mm long. Texture coriaceous; color pale green (alive). Venation free, the veinlet trusses in proximal blade segments usually producing 4–5 endings. Glands absent. Sori round, mostly 5–7, 0.5–1.0 mm in diameter with reniform indusia. Spores normal. Chromosome number: $n = 123$.

HOLOTYPE: E. Maui. Haleakala. Koolau Gap. Ainahou Valley. Ca. 1550 m. Growing with much more common *D. wallichiana*. 10 Aug. 1965. *Wagner 65450* (1 frond on 3 sheets–MICH).

Other collections: E. MAUI: Haleakala. Wai Anapanapa, Kipahulu-Kuhewa Divide. 2000 m. Rainforest at tree line. 16 Aug. 1945. *St. John & Mitchell 21034* (US). Paliku, woods, 4 June 1955. *Degener et al. 27406* (US). Keanae Gap. Halehaku. 2 Aug. 1919. *Forbes 971M* (US).—W. MAUI: Between Haelaau and summit of Puu Kukui, along trail near bogs. 25 July 1965. *Wagner 65392* (MICH).

This striking fern (Fig. 4) remained unnoticed until the senior author recognized its distinctive features in the 1940's. Collectors have identified it as *Polystichum hillebrandii*, *Dryopteris paleacea*, *D. fusco-atra*, and *D. hawaiiensis*. In his earlier Hawaiian checklists, Wagner gave it the provisional name "*D. pseudopaleacea*," but the name *D. wallichiana* (Spreng.) Hyl. has nomenclatural precedence over *D. paleacea* (Sw.) C. Chr. The following key places *D. subbipinnata* in comparison with what are its most similar relatives.

1. Rachis scales grayish to blackish, mostly less than 1 cm long; upper pinnae usually not overlapping rachis, gradually narrowing from base to apex; lower pinnae only slightly reduced; medial veins mostly unbranched; sori mostly 2–4 pairs per segment. *D. fusco-atra.*
1. Rachis scales orange-brown to dark chestnut, the largest reaching over 1 cm long; upper pinnae usually overlapping rachis, almost parallel-sided in lower 2/3; lower pinnae commonly 1/3 to 2/5 the length of the medial pinnae; medial veins mostly 1–3-branched; sori mostly 4–7 pairs per segment.
   2. Medial and lower pinnae not overlapping; segments in lower part of blade completely adnate, 8–12 × 2–4 mm, unlobed, sharply truncate; segment vein trusses with 2–3 endings. *D. wallichiana.*
   2. Medial and lower pinnae overlapping; segments in lower part of blade more or less contracted or stalked at base, 15–25 × 5–10 mm, shallowly to deeply lobed, rounded at apex; segment vein trusses with 4–5 endings. *D. subbipinnata.*

Grammitis forbesiana W. H. Wagner, sp. nov.

G. hookeri simulans sed soris in medio laminae et lamina in stipite 0.5–2.0 cm longo gradatim decrescenti; pili in lamina stipiteque pro parte maxima 0.5–2.0 mm longi; sporae 80–100 μm in diametro.

Tufted epiphyte. Rhizome upright, 0.5–1.3 × 0.2–0.4 cm. Stem scales densely overlapping, pale tan concolorous, 2.0–3.0 × 0.3–0.4 mm, with scattered minute capillary hairs. Roots very narrow, black, branched. Frond linear 10–17 × 0.5–1.0 cm. Hairs on blade and stipe frequent to common, stiff black, 0.5–2.0 mm long. Stipe wiry, dark brown mostly 0.5–2.0 cm. Blade simple, narrowed apically and basally, reducing gradually to stipe. Margins entire. Texture thick, fleshy, dark green, blade readily cracked when bent. Sori medial, subelliptic in early development becoming circular at maturity. Capsule paraphyses 1–2 minute stiff black hairs, frequent to sparse. Spores spherical, diameter mostly 80–100 μm.

FIG. 4. *Dryopteris subbipinnata* W. H. Wagner & R. W. Hobdy. Maui, Upper Waikamoi Forest; *Wagner 87135* (MICH). Central part of blade. Note overlapping, lobed segments.

HOLOTYPE: W. Maui. Trail between Haelaau and summit of Puu Kukui. 25 July 1965. *Wagner 65386* (MICH).

Other collections: OAHU: Koolau Range; Hauula Range, Kaluanui Stream. 500–600 m. 31 Aug. 1947. *Wagner 5767* (MICH).—MOLOKAI: No locality. *Rock 6161* (MICH); Near Hanilolilo, S rim of Waikolo Valley. 5 July 1964. *Crosby & Anderson 1683* (MICH); Pukoo. July 1912. *Forbes 271Mo* (MICH).—W. MAUI: Puu Kukui, woods above Haelaau. 1200 m. 29 June 1948. *Wilbur & Webster 926* (MICH); *Hitchcock 14766* (US); Gulch and ridge overlooking Hokuula, 1 mi N of Puu Anu. 25 July 1947. *Wagner 5395* (MICH). E. MAUI: Flume Trail. Olinda Water Reserve. 16 August 1951. *H. L. Bonsey 2196* (MICH); 20 April 1963. *Sparrow & Bonsey* (MICH); Olinda Flume, Waikamoi. 16 July 1964. 1200 m. *Crosby & Anderson 1758* (mixed with *G. hookeri*, MICH).

This previously overlooked fern is obviously intermediate between *Grammitis baldwinii* (Baker) Copel., a species known today only from Kauai, and *G. hookeri*, widespread throughout the islands. The most conspicuous intermediate characters are soral position, frond shape, stipe length, hair incidence and length, and paraphyses. E. B. Copeland noted the soral position. He annotated the Hitchcock specimen in the U.S. National Museum "sori remote from costa." Hillebrand had observed this earlier; his "β var." of *Polypodium hookeri* (1888, p. 553) described the sori as "midway between rib and edge" as opposed to taxon *hookeri* with sori "forming two rows close to the midrib."

1. Sori submarginal; stipe very short, usually less than 1/30–1/8 of the frond length; frond essentially glabrous except at base; capsular paraphyses abundant in sori. *G. baldwinii.*
1. Sori medial or costal; stipe larger mostly 1/15–1/3 of the frond length; frond with numerous and conspicuous stiff, black hairs; capsular paraphyses frequent to sparse in sori.
   2. Sori medial; lamina subcoriaceous reducing gradually to stipe mostly 0.5–2.0 cm long; hairs on blade and stipe frequent to common, mostly 0.5–2.0 mm long; spore diameter 80–100 µm. *G.* [×] *forbesiana.*
   2. Sori costal; lamina chartaceous reducing more abruptly to stipe mostly 1–6 cm long; hairs on blade and stipe common to abundant, mostly 2–3 mm long; spore diameter 60–75 µm. *G. hookeri.*

×**Lindsaeosoria flynnii** W. H. Wagner, nothogen. et nothosp. nov.

Planta inter *Lindsaeam ensifoliam* et *Odontosoriam chinensem* intermedia; lamina 2-pinnata, prope medium abrupte decrescens; pinnae crispatae; lamina pinnaeque ambito maxime irregulares; pinnulae stipitatae pinnae basalis 1–4; sporae abortivae.

Hybrid between *Lindsaea ensifolia* and *Odontosoria chinensis*. Tufted terrestrial fern with spreading to upright fronds. Rhizome short-creeping, 1–2.5 mm thick. Stem fibrils very narrow, several cells wide at base, reddish brown. Fronds including stipe 10–45 × 3–7 cm. Stipe 3–15 cm long. Blade narrowly lanceolate, 1 (–2)-pinnate, the tip attenuate, usually reduced abruptly beginning at middle of blade. Pinnae 1.0–10.0 × 0.5–2.0 cm with stalks up to 2 mm long. Pinna bases cuneate, gradually contracting to stalk. Lamina thick chartaceous, pale green. Stalked pinnules on basal pinna 1–4. Venation free except for rare anastomosis of veins under fused sori. Sori mainly separate, 0.3–0.9 mm long. Indusium 0.3–1.5 mm long (in fused sori). Spores abortive.

HOLOTYPE: Kauai, northeast of Keahili Mt. Park, in an abandoned litchi orchard. 12 April 1987. *Wagner 87211* (MICH).

Other collection: Same locality. 26 August 1987. *Flynn 2351* (MICH, PTBG).

FIG. 5. ×*Lindsaeosoria flynnii* W. H. Wagner (center). *Lindsaea ensifolia* (left) × *Odontosoria chinensis* (right). Kauai, N.E. Kahili Mt. Park; *Wagner 87211* (MICH).

This extraordinary natural hybrid (Fig. 5) combines in a peculiar way the characters of its parents, making it unusually interesting morphogenetically. Some of the characters, as shown in Table 1, are like *Odontosoria chinensis* (L.) J. Sm. (e.g., free veins), or intermediate with *Lindsaea ensifolia* Sw. (e.g., pinna stalk length); others are unlike either parent (e.g., pinna bases). In general the hybrid seems more like *Odontosoria*. The latter, it should be noted, has the majority of primitive or plesiomorphous characters, and they appear to dominate in the hybrid (cf. Wagner 1962).

Microlepia mauiensis W. H. Wagner, sp. nov.

A *M. strigosa* frondibus utrinque dense pubescentibus differt; rachides costaeque flexuosae; segmenta 2–3plo longiora quam latiora, rotundata.

Medium- to large-sized, hairy terrestrial rainforest fern. Rhizome creeping, the fronds borne at intervals of 0.8–1.0 cm. Rhizome tip with uniseriate hairs densely massed, 1–3 mm long, white to brown. Frond elongate-deltate, up to 100 × 30 cm, including stipe. Stipe up to 50 cm, more or less densely hairy. Blade 3-pinnate, tip formed by gradual reduction. Rachis 1.5 (1.2–1.8) mm thick 20 cm from frond apex. Rachis and costae mostly flexuous, densely hairy, brownish (due to admixture of partially or wholly pigmented hairs). Pinnae linear-deltate, narrowing uniformly from base. Segments ovate to oblong, usually 2–3× as long as broad, the apices somewhat rounded. Lamina chartaceous, hairy both below and above, the hairs on adaxial side not confined to margins. Color pale green, but dull due to numerous hairs. Venation free. Sori submarginal, on tips of veins that do not reach margin. Indusium semicircular, opening outward, hairy, attached at base.

TABLE 1. Comparison of an intergeneric hybrid with its parents.

	Odontosoria chinensis	×*Lindsaeosoria flynnii*	*Lindsaea ensifolia*
Occurrence	Usually by itself	Only with parents	Usually by itself
Incidence	Abundant	Only 8 plants seen	Abundant
Patchiness	Separate	Separate	Continuous clones
Fronds	Tufted	Tufted	Not tufted
Orientation	Spreading	Spreading to upright	Upright
Petiole	Pale pink	Purple	Purple
Blade cutting	3-pinnate	2-pinnate	1-pinnate
Tip formation	Gradual reduction in symmetry	Sudden reduction at middle of blade	Conform terminal pinna
Exaggerated basal pinna pairs	0	1–3	1–6
Basal pinna orientation (alive)	Spreading	Nearly erect	Erect
Lamina	Smooth	Crispate	Smooth
Symmetry	Regular	Highly irregular	Regular
Pinna stalk (mm)	2–3	1–2	0.5–1
Stalked pinnule pairs on two basal pinnae	6–16	0.5–2	0
Pinna bases	Abruptly contracted	Gradually tapered	Abruptly tapered
Ultimate pinnae and segment shapes	Cuneate	Cuneate to flabellate	(No secondary segments)
Number of veins in ultimate segments or lobes	2–4	3–12	(No secondary segments)
Venation	Free	Free (marginal fusions rare)	Reticulate (1–3 layers of areoles)
Sorus	Discrete, 0.3–0.9 mm	Discrete, 0.3–0.9 mm, to rarely fused, up to 1.5 mm	Coenosoral
Soral margin	Plane	Somewhat revolute	Revolute
Spores	Normal	Abortive	Normal

HOLOTYPE: W. Maui. Hanaula. In wet forest above reservoir. Hairy form with zig-zag rachis. 1279 m. 25 March 1984. *Wagner et al. 87107a* (2 sheets, MICH).

Other collections: W. MAUI: Type locality. 31 Oct. 1984. *Hobdy 2206* (MICH). Mauna Wainui Plant Sanctuary. 850 m. 1983. *Hobdy 1848* (BISH). Upper Poe Lua Gulch. 425 m. 1984. *Hobdy 2091* (BISH).—E. MAUI: Yhou Gulch, above Makawao. 1035 m. 1980. *Hobdy 766* (BISH).—HAWAII: Manuka, in kipuka. 1400 m. 1977. *P. Higashino 6219* (BISH). Puu Makalua. 1991. 1310 m. *Palmer 636* (BISH). Kau Forest Reserve, above Kapapala Forest Reserve. 1310 m. 1991. *Palmer 624* (BISH).

This very rare and local taxon (known at present only from Maui and Hawaii) differs in so many conspicuous characters (Fig. 6) from the abundant and widespread *M. strigosa* (Thunb.) Presl that it cannot be maintained as a variety, even though occasional plants of the latter show some apparent introgression toward it. The following key will distinguish the rare from the common species.

Fronds sparsely hairy, the rachises and costae whitish yellow or green at maturity; rachis 1.3 (0.8–1.6) mm thick 20 cm from frond apex; rachises and costae non-flexuous; segments mostly 2.5–4.0× as long as broad, more pointed, hairy only on abaxial side or if hairy on adaxial side the few hairs usually submarginal; elevation widely variable from near sea level upward, habitats mostly dry to moderately wet. *M. strigosa.*

Fronds densely hairy, the rachises and costae reddish brown at maturity; rachis 1.5 (1.2–1.8) mm thick 20 cm from frond apex, but appearing thicker due to dense hairs; rachises and costae flexuous; segments mostly 2–3× as long as wide, rounded, strongly hairy on both surfaces, the hairs not only submarginal; elevations around 1200 m or above, habitat extremely wet. *M. mauiensis.*

Polystichum bonseyi W. H. Wagner & R. W. Hobdy, sp. nov.

A *P. haleakalensi* pinnis proximalibus quam pinnis medianis plerumque fere aequilongis differt; squamae rhizomatis stipitisque rubellae et in medio vulgo vitta atra instructae; exospora 50 (40–60) μm longa.

Coarse fern of mainly open rocky habitats. Rhizome compact, short, creeping, the apex and petiole bases densely covered with pale tan scales up to 1.0 × 0.5 cm, a few of the larger ones with irregular longitudinal medial streaks of shiny blackish brown. Scales becoming smaller and narrower in upper petiole, forming fibrils 1.0–3.0 × 0.1–0.3 mm. Blade bipinnate, up to 100 × 12 cm, narrowly lanceolate, but the lowest pinna pairs usually nearly or quite unreduced, approximately equal in length (only occasionally reduced to 2/3) to the middle pinnae. Rachis densely reddish fibrillate. Lamina chartaceous, the upper surface glabrous, the lower with scattered long multicellular hairs. Margin not strongly cartilaginous, strongly spinulose, with 7–11 projections per pinnule, these mainly 0.5–1.0 mm long. Pinnules 0.8–1.3 cm long, but the first acroscopic pinnule 1.0 –1.3× the length of the second acroscopic pinnule. Angle of the pinnules ca. 40°–50° to the costa. Sori ca. 1 mm across when mature. Indusia becoming folded (when dry) margins somewhat irregular due to projection of 1-celled hairs. Spores 40–60 μm long. Chromosome number: $n = 164$.

HOLOTYPE: E. Maui. W side of Puu Nianiau, steep rocky gulch. 2000 m. 9 July 1947. *Wagner 5226* (MICH).

Other collections: E. MAUI: Crater Road, in a gulch above the road, 1900 m. 3 Mar. 1985. *R. Hobdy 2295* (BISH); Plum Trail, Polipoli. 1700 m. (3 specimens) *R. Hobdy 377* (BISH); Kula, in a shady gulley near the Polipoli Access Road, 1700 m. In company with *P. hillebrandii*. 17 Apr. 1984.*R. Hobdy 2061* (BISH). Eastern Outer Rim of Haleakala Crater, 2 mi NE of Paliku Cabins, in shaded rainforest along ridge north of Wai Anapanapa. Rosette fern at edge of deep gulch with *Metrosideros*, *Pelea*, *Myrsine*, *Rubus*, *Cheirodendron*, *Coprosma*, *Sadleria*, *Styphelia*. Common. 2000 m. 18 June 1969. *Henrickson & Vogl 3520* (BISH).—HAWAII: N. Kona. Hualalei. Plants growing in

FIG. 6. *Microlepia mauiensis* W. H. Wagner. E. Maui, Hanaula; *Wagner 87107a* (MICH). Note thick flexuous rachis.

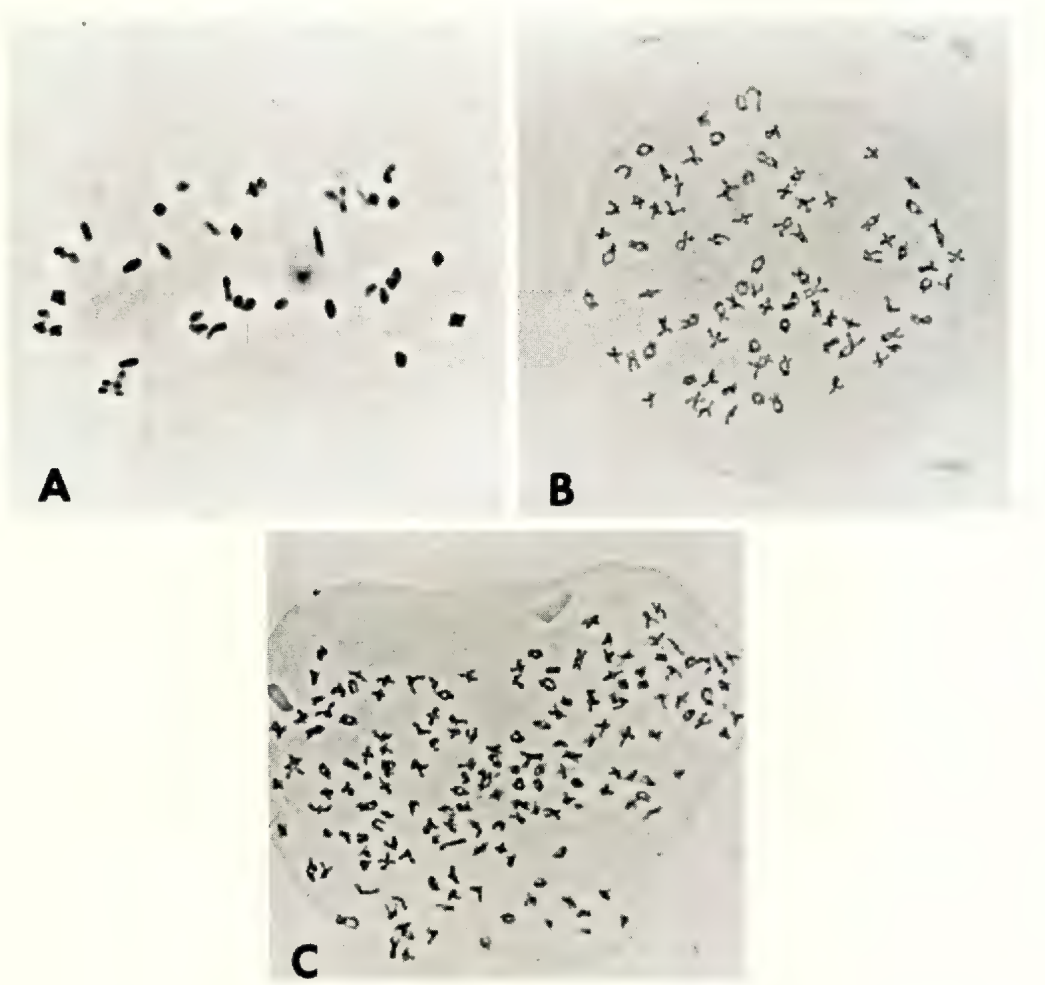

FIG. 7. Chromosomes of Hawaiian *Polystichum*. A. *P. hillebrandii*, $n = 41$; B. *P. haleakalense*, $n = 82$; C. *P. bonseyi*, $n = 164$.

very deep cinder cone, water dripping from side, moist area. Vegetation: *Metrosideros, Raillardia, Stenogyne, Styphelia*. 26 Nov 1977. *Higashino 6623* (BISH).

We have only a single record from the island of Hawaii. It is interesting to note that the only occurrence is on Hualalei, not on either Mauna Kea or Mauna Loa. In Maui, *Polystichum bonseyi* is found throughout the mesic forest zones of the south and west slopes of Haleakala and well up into the subalpine zones as well. It also occurs in the rainforest-subalpine ecotone across the north slope and east end of the crater. Here it reaches its best development (in size and vigor but not in numbers). The plants prefer open sunny ledges near gulch bottoms but also occur in forest understory in gulch bottoms and occasionally on ridgetops in the wetter part of its distribution. Of the three species of Hawaiian *Polystichum*, this is perhaps the commonest. In ideal sites it sometimes becomes gregarious, usually associated with *Dryopteris wallichiana*. The elevational range of *Polystichum bonseyi* is 1400–2000 m, and the rainfall range is 40–100 inches. The three native species of this genus differ in chromosome number: *P. hillebrandii* Carruth., $n = 41$; *P. haleakalense* Brack., $n = 82$; and *P. bonseyi*, $n = 164$ (Fig. 7).

1. Fronds very leathery, shiny; pinnule margins cartilaginous, marginal projections absent or small; largest petiole scales broadly ovate, very large and overlapping; indusium with nearly entire margin; exospores 30 (25–35) μm long. *P. hillebrandii.*
1. Fronds papery or herbaceous, dull; pinnule margins non-cartilaginous with strong marginal projections; largest petiole scales narrow, lanceolate and interspersed with linear fibrils; indusium with marginal projections; exospores various in length.
   2. Lower pinnae usually reduced to 1/3 or 1/4 the length of the medial pinnae; rhizome and lower stipe scales pale whitish gray or brown, concolorous; exospores 35 (25–45) μm long. *P. haleakalense.*
   2. Lower pinnae usually nearly equal to the length of the medial pinnae; rhizome and lower stipe scales more reddish, and commonly with a dark stripe; exospores 50 (40–60) μm long. *P. bonseyi.*

Pityrogramma [×] **mckenneyi** W. H. Wagner, nothosp. nov.

Planta inter *P. austroamericanam* et *P. calomelanos* intermedia; a *P. calomelanos* farina flavido-alba differt; auriculae pinnularum magnarum usque ad 1 mm longae; porcae adaxiales rachidis atropurpureae tantum in tertio proximali; sporae abortivae.

Tufted medium-sized terrestrial fern of weedy places. Rhizome upright 2.0 × 1.0 cm including stipe bases and roots. Stem scales extremely narrow, 4.0–6.0 × 0.1–0.3 mm at base, becoming 1–2-celled in upper 1/3–2/3. Roots narrow, black, few-branched, producing proliferations. Fronds somewhat spreading, broadly lanceolate, up to 105 × 20 cm including shiny, dark glabrous stipe up to 35 cm. Blade oblong-lanceolate, bipinnate to tripinnate. Rachis green except for dark purple color on adaxial ridges in lower third. Pinnae attenuate triangular 3.0–10.0 × 1.0–2.0 cm, with stalks up to 3.5 mm. Pinnules in proximal area shallowly auricled; pinna tips more or less pointed; margins subdentate. Texture subcoriaceous. Adaxial lamina surface shiny green, the cells long and narrow, fiberlike; abaxial surface pale whitish yellow due to numerous globular farina glands. Sorus acrostichoid, the sporangia scattered, non-indusiate. Spores abortive.

HOLOTYPE: Oahu. Kaneohe, Hoomaluhia Botanical Garden. On hillside above Loho Wainaluhia Reservoir. Extremely abundant, with parents. March 1987. *Wagner 87173* (MICH).

A beautiful, very vigorous intermediate between the silverback fern, *Pityrogramma calomelanos* (L.) Link, and the goldback, *P. austroamericana* Domin, to be expected wherever the parents co-occur. In spite of its sterility, it is reproductively competent, producing colonies by its strong ability to propagate by roots. It is here keyed out with its parental species.

1. Farina deep golden yellow; mature living plant with spreading leaves; blades mostly bipinnate; basal pinnules usually not auricled; segment tips usually rounded; margin entire to subentire; lowest pinnae with stalks 4–6 mm long; usually only the lower 1/4 to 1/5 of the adaxial ridges on the midrib dark purple, the remainder greenish; texture subcoriaceous. *P. austroamericana.*
1. Farina white or whitish yellow; mature living plant with upright to somewhat spreading leaves; blades tripinnate to bipinnate; large basal pinnules usually auricled; segment tips more pointed; margins subdentate to dentate; lowest pinnae with stalks 2–5 mm long; the lower 1/3 to 2/3 of the adaxial ridges on the midrib dark purple, the remainder greenish; texture subcoriaceous to chartaceous.
   2. Farina pure white; lower half or more of the adaxial ridges on the midrib dark purple; auricles on large pinnules up to 2 mm long, pointed; spores normal. *P. calomelanos.*
   2. Farina pale whitish yellow; lower third of adaxial ridges on the midrib dark purple; auricles on large pinnules mostly smaller and rounded; spores abortive. *P.* [×] *mckenneyi.*

Psilotum [×] **intermedium** W. H. Wagner, nothosp. nov.

Planta inter *P. complanatum* et *P. nudum* intermedia; a *P. nudo* ramis partialiter arcuatis, irregulariter planis vel in sectione transversali triangularibus differt; sporangia 2- vel 3-seriata; sporae abortivae.

Tufted terrestrial or epiphytic plants with essentially naked axes. Roots absent. Buried stems mostly 2–3 mm thick, brown with short horizontal branches provided with numerous rhizoids, and upright aerial branches mostly 1.5–2.5 mm thick, green. Typical leaves absent, the upright stems provided with minute simple enations mostly 1–2 mm long. Branchlets varying from nearly upright spreading, to more or less pendent, in cross section from flat and ribbonlike to triangular and cordlike. Sporangia borne terminally on forked appendages slightly larger than the simple sterile appendages. Sporangia very large 1.5–2.0 mm in diameter, fused into tight 3-lobed synangia. Spores abortive, mostly empty, and of diverse sizes and shapes.

HOLOTYPE: Oahu. Waianae Mountains, Kanehoa Trail, SW of Kunia, with parents. Frequent in moss on ridge. 27 August 1961. Wa*gner 9615a et al.* (MICH).

Other collections: MAUI: Kipahulu. Summit of west ridge of Kaukana Gulch. Koa woods, at base of koa tree. 500 m. 28 December 1936. *St. John 17811* (MICH).—KAUAI: NW of Kalahao, Kanela Swamp. 650 m. *J. Henrickson 4000* (US).—LANAI: SE of Haalelepaahu, Monaneo Gulch. 850 m. *O. Degener & I. Degener 31151* (US).

The two species of *Psilotum* in Hawaii are remarkably common, *P. nudum* (L.) Beauv. being found even in downtown Honolulu, especially at bases of coconut palms, but *P. complanatum* Sw. is limited to higher altitudes and shadier and moister native habitats. The hybrid (Fig. 8) is widespread and may be expected anywhere that both species occur near each other. The hybrid plants were first noted in 1961, and first reported and illustrated by Wagner in 1968. In some localities the hybrids are quite common, as along certain mossy trails in the Waianae Mountains of Oahu. Presumably their reproduction and dispersal is accomplished by tiny gemmae (brood bodies) produced underground near the rhizome tips.

1. Branchlets mostly strongly arched, entirely flat, their width almost uniform to the apex, 2.3–3.0 mm wide; sporangia 2-ranked in parallel rows on opposite sides of the branchlets; primary aerial stalk 25–70% of length of the branchlet cluster. *P. complanatum.*
1. Branchlets somewhat arched or straight and erect, flat to triangular in section, their width more or less diminishing in distal 5–10 cm, 0.7–2.3 mm wide; sporangia 2-ranked to irregularly or regularly borne around the branchlets; primary aerial stalk 50–300% of the length of the branchlet cluster.
   2. Branchlets partially arched, irregularly flat to triangular in section, their width strongly varying with the outline ca. 1.0–2.5 mm, sporangia fluctuating from 2- to 3-ranked; spores abortive. *P.* [×] *intermedium.*
   2. Branchlets nearly upright, usually not arched except in very large luxuriant epiphytes, regularly triangular in section, their width 0.7–1.2 mm; sporangia mainly 3-ranked; spores normal. *P. nudum.*

Thelypteris ×**incesta** W. H. Wagner, nothosp. nov.

Planta inter *T. dentatam* et *T. parasiticam* intermedia; a *T. dentata* 1–2 paribus pinnarum proximalium redactis, pinnis infimis 5plo longioribus quam latioribus, differt; rachis raro purpurea; segmenti secunda venula antica basi vel supra basim

FIG. 8. *Psilotum* [×] *intermedium* W. H. Wagner (*P. complanatum* × *P. nuda*). Oahu, Waianae Mts. sw of Kunia. Note irregular branch form alternating from flat to 3-angled. (Photograph by Sherwin Carlquist.)

sinus finem habens; glandulae aurantiacae globularesque tantum aliquando praesentes; sporae abortivae; $4x = 144$, sterilis.

Intermediate between *T. dentata* and *T. parasitica*. Medium-sized terrestrial weedy fern with leaves 2–8-tufted on a creeping rhizome. Rhizome 1.0–2.0 cm thick, usually with several old stipe bases. Stem tip scales brown, linear, 4.0–8.0 × 0.5–1.0 mm at base, reducing to a long narrow distal portion. Roots abundant and much branched, 0.5 mm thick down to capillary. Fronds 70–150 × 25–35 cm including stipe. Stipe 20–50 cm long and with few scales like those of rhizome but smaller, scattered on basal 5 cm. Blade lanceolate-oblong, 1-pinnate, with pinnatifid pinnae, 25–35 pairs. Medial pinnae sublinear 7.0–14.0 × 1.4–2.0 cm, cut 1/3–2/3 into segments. Frond apex reduced to a prolonged narrowing tip 5–10 cm long. Basal pinnae frequently somewhat falcate and descending, usually only 1–4, reduced. First rachial sector 5.4 (4.0–8.5) cm. Lamina texture chartaceous, green. Second lateral veinlet on anterior side reaching to or slightly above the sinus base. Sinuses narrow. Minute golden globular glands occasional on abaxial surface of costae. Spores abortive. Chromosome number: $4x = 144$, pairing irregular.

HOLOTYPE: Kauai: Wahiawa. Road below Alexander Dam. Occasional with parents. 10 April 1987. W*agner 87191* (MICH).

Other collections. E. MAUI: Hanawa Valley , along road from Hanawa Parking Place to Hana Road. 100 m. 28 March 1987.*Wagner 87170.5a* (MICH). OAHU: Koolau Mountains. Mt. Tantalus. Manoa Cliff Trail. Large clone with parents. 4 February 1987. *Wagner 87020* (MICH).

This is probably a relatively common nothospecies throughout the islands, due partly to the abundance of the parents in disturbed places. It tends to grow taller and more vigorously than either of its parents, and this helps in its field recognition. The differences of the hybrid from its parents are rather subtle, and only recently have we been able to detect it easily. Holttum (1977) did not report hybrids between *T. dentata* (Forsk.) E. P. St. John and *T. parasitica* (L.) Fosberg, which themselves are well known, widespread tropical weeds and commonly occur side-by-side in the same habitats.

1. Lower pinnae little or not reduced, linear, the basal ones approximately the same length as the medial ones, and prominently curved upward; first rachial sector averaging 2–3 cm long; medial pinnae usually narrow and cut about 1/2–2/3; lamina color above (alive) yellowish green; rachis color pale green to yellowish; partially fertile pinnae common, with paired sori along the costa; second anterior veinlet usually ending above the base of the sinus; sinuses wide; minute spherical orange glands scattered on the abaxial costae. *T. parasitica.*
1. Lower pinnae definitely reduced, usually 1–4 pairs, the lowest usually 1/2–1/5 as long as the medial ones, mostly not curved; first rachial sector averaging 4–7 cm long; medial pinnae usually broader and cut 1/2–1/3; lamina color above darker than below (alive); rachis color green to purple; partially fertile pinnae with paired sori along costa not common; second anterior veinlet variously ending at or above the base of the sinus; sinuses narrow; minute glands present or absent.
   2. Lower pinnae, usually 1–2 pairs, reduced, the lowest variable in size but averaging approximately 5× as long as wide; first rachial sector mostly 4.5–6.0 cm; lamina color above green; rachis rarely purple; second anterior veinlet ending at or above the base of the sinus; occasional minute orange glands on abaxial costae; spores abortive. *T. ×incesta.*
   2. Lower pinnae, usually 1–4 pairs, reduced, the lowest variable in size but averaging approximately 2.5× as long as wide; first rachial sector mostly 5.5–7.0 cm; lamina color above dark green; rachis commonly purple; second anterior veinlet ending usually at the base of the sinus; glands absent on abaxial costae; spores normal. *T. dentata.*

Thelypteris [×] **palmeri** W. H. Wagner, nothsp. nov.

Planta inter *T. dentatam* et *T. cyatheoides* intermedia; a *T. dentata* fronde 1–2 m alta differt; basis petioli 5–10 mm crassa; rachidis sulcus 2–4 mm latus; pinnae 1/3 fissae, lobis 30–45; paria venarum 6–8 per segmentum, infimum a costa abiens; vena commissuralis flexuosa; sporae abortivae; $3x = 123$, abortiva.

Medium to large weedy fern forming extensive clones. Rhizome creeping, 9–12 mm thick. Scales tufted at apex of stem and crosier, dark gray-brown, elongate-triangular, 3.0–6.0 × 0.5–1.5 mm. Frond narrowly lanceolate, contracted below, 1.0–2.0 × 0.3–0.5 m. Petiole 30.0–50.0 × 0.4–0.9 cm. Middle pinnae 12.0–15.0 × 1.7–2.2 cm, nearly parallel-sided, narrowing in outer third. Blade apex formed by gradual reduction; 3–6 basal pinna pairs reduced. Lobes mostly 30–45 in middle pinnae, rounded, slightly or not at all falcate, 6–8 vein pairs per lobe, the lowest pair beginning at costa, the commissural vein somewhat zig-zag. Sinuses cut 1/3 to 1/2. Fusion of veins of adjacent lobes irregular. Lamina chartaceous, somewhat shiny. Spores abortive. Chromosome number: $3x = 108$, pairing irregular.

HOLOTYPE: Oahu. Koolau Mountains. Palolo Valley Trail up to waterfalls. 1 February 1987. *Wagner 87013* (MICH).

Other collection: OAHU. Mt. Tantalus, north side, along cross-trail. 10 May 1987. *Wagner 87223* (MICH).

This hybrid of *Thelypteris cyatheoides* (Kaulf.) Fosberg and *T. dentata* forms large, widely scattered clones. It is probably much more common than the collections would indicate. It should make a showy, if aggressive, cultivated plant.

Thelypteris [×] *palmeri* is a fine example of a nothospecies that resembles its parent with the tetraploid chromosome number, *T. dentata*, rather than the one with the diploid number, *T. cyatheoides*. For this reason the hybrid is compared with *T. dentata* in the following key.

Fronds 0.5–1.0 m long; pinnae cut 1/2 into 15–25 lobes, each with 5–7 vein pairs; first vein pair arising 0.5 mm from costule; commissural vein mainly straight. *T. dentata.*

Fronds 1.0–2.0 m long; pinnae cut 1/2–1/3 into 30–45 lobes, each with 6–8 vein pairs; first vein pair arising at costule; commissural vein somewhat zig-zag. *T.* [×] *palmeri.*

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CHROMOSOMES OF NORTH AMERICAN GRAPEFERNS AND MOONWORTS (OPHIOGLOSSACEAE: BOTRYCHIUM)

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Because of rarity and small size, and the resulting inconspicuousness, the diversity of moonwort species (*Botrychium* subg. *Botrychium*) has been largely overlooked by botanists, until the last 15 years. Intensive work since 1977 has resulted in discoveries, descriptions, and reinterpretations of 16 species to be added to the seven known before.

Scattered reports of chromosome numbers in a few of the more common moonworts have appeared in the past. Many of these, however, have been published without voucher citations and have lacked illustrations of the chromosomes. Table 1 gives chromosome numbers for all of the described North American botrychiums, with the exception of *Botrychium gallicomontanum* (Farrar & Johnson-Groh 1991). Photographs and, in two cases, interpretive drawings of those taxa not previously illustrated are shown in Figs. 1–4.

A number of the new species whose chromosome numbers are given here are found only in the western mountains of North America, and many grow at high altitudes. The stages of sporogenesis suitable for meiotic counts occur early in the spring, and in the mountain habitats, snow-covered roads make collecting chromosome material prohibitive. In order to solve this problem our method was to collect clumps of soil containing mature moonworts during the summer collecting fieldwork. The soil clumps in plastic bags were kept in a Cold Temperature Room (40° F) during the winter, and in the spring placed in empty covered glass aquaria outdoors. Each clump was watered on alternate days. The botrychiums would emerge, produce young sporangia, which were fixed in Newcomer's Solution, and then be collected as vouchers if they matured. We have found it difficult, if not impossible, to cultivate these plants for more than a year, but we were ultimately successful using this method in obtaining chromosome numbers for all the western species and also for those that occur in the Lake Superior area.

The cytological procedure consisted of placing young sporangia on a microscope slide in a drop of ACH (50% aceto-carmine, 50% Hoyer's Solution), teasing and removing the sporangial walls, and, after covering with a cover slip, gently squashing the remaining contents. Good figures were photographed with a compound microscope under an oil immersion 100× objective, or a 40× high dry objective if the figure was too large. Interpretive drawings were made with a drawing tube to facilitate counting the chromosomes. Slides were sealed first with nail polish and then, after a week, with Glyptal (a sealant made by General Electric). In the case of *B. montanum,* the only figure obtained was photographed but could not be drawn; the number is therefore approximate. The chromosomes of *B. crenulatum*, on the other hand, are shown in a drawing, the figure not surviving to be photographed.

TABLE 1. Chromosome numbers in North American botrychiums. All Wagner vouchers are deposited at MICH.

Species	Locality	Chromosome Number	Ploidal Level	Reference
Botrychium subg. *Osmundopteris*				
B. virginianum (L.) Sw.	MI: Washtenaw Co., *Wagner* on May 15 1954	$n = 92$	4*x*	Wagner 1955
Botrychium subg. *Sceptridium*				
B. biternatum (Sav.) L. Underw.	IN: Jefferson Co., *Wagner 9273*	$n = 45$	2*x*	Wagner 1963
B. dissectum Spreng.	*Britton s.n.*	$n = 45$	2*x*	Britton 1953
B. jenmanii L. Underw.	AL: Mobile Co., *Beibel 9213*	$n = 90$	4*x*	Wagner 1963
B. multifidum (Gmel.) Rupr.	MI: Washtenaw Co., *Wagner* on 22 June 1954	$n = 45$	2*x*	Wagner 1955
B. oneidense (Gilb.) House	MI: Washtenaw Co., *Wagner* in 1954.	$n = 45$	2*x*	Wagner 1955
B. rugulosum W. H. Wagner	MI: Monroe Co., *Wagner 9067*	$n = 45$	2*x*	Wagner & Wagner 1982
B. lunarioides (Michx.) Sw.	AL: Lee Co., *Wagner 9195*	$n = 45$	2*x*	Wagner 1963
Botrychium subg. *Botrychium*				
B. acuminatum W. H. Wagner	MI: Alger Co., *Wagner 85043*	$n = 90$	4*x*	Wagner & Wagner 1990b
B. ascendens W. H. Wagner	OR: Wallowa Co., *Wagner 83363*	$n = 90$	4*x*	Wagner & Wagner 1986
B. campestre W. H. Wagner & Farrar	MI: Leelanau Co., *Wagner 85025*	$n = 45$	2*x*	Wagner & Wagner 1986
B. crenulatum W. H. Wagner	CA: San Bernardino Co., *Kiefer* on 15 Aug 1963	$n = 45$	2*x*	Wagner & Wagner 1981
B. echo W. H. Wagner	CO: Clear Creek Co., *Wagner 82135*	$n = 90$	4*x*	Wagner & Wagner 1983
B. gallicomontanum Farrar & Johnson-Groh	MN: Norman Co.	unknown	4*x*	Farrar & Johnson-Groh 1991

TABLE 1 continued.

B. hesperium (Maxon & Clausen) W. H. Wagner & Lellinger	CO: Clear Creek Co., *Wagner 82136*	*n* = 90	4*x*	Wagner & Wagner 1983
B. lanceolatum (Gmel.) Angstr. ssp. *lanceolatum*	WA: Skamania Co., *Wagner 63112*	*n* = 45	2*x*	Wagner in Fabbri 1963
B. lanceolatum ssp. *angustisegmentum* (Pease & Moore) Clausen	MI: Emmet Co., *E. G. Voss* on 15 May 1954	*n* = 45	2*x*	Wagner 1955
B. lunaria (L.) Sw.	MI: Chippewa Co., *Wagner 8199*	*n* = 45	2*x*	Wagner & Lord 1956
B. matricariifolium A. Br.	MI: Emmet Co., *Wagner* in 1955	*n* = 90	4*x*	Wagner & Lord 1956
B. minganense Victorin	MI: Chippewa Co., *Wagner 8200*	*n* = 90	4*x*	Wagner & Lord 1956
B. montanum W. H. Wagner	MT: Lake Co., *Wagner 80110*	2*n* = ca. 90	2*x*	Wagner & Wagner 1981
B. mormo W. H. Wagner	MN: Clearwater Co., *Wagner 77326*	2*n* = 90	2*x*	Wagner & Wagner 1981
B. pallidum W. H. Wagner	MI: Chippewa Co., *Wagner 89041*	2*n* = 90	2*x*	Wagner & Wagner 1990a
B. paradoxum W. H. Wagner	AB: Waterton Lakes Natl. Park , *Wagner 83331*	*n* = 90	4*x*	Wagner & Wagner 1981
B. pedunculosum W. H. Wagner	OR: Wallowa Co., *Wagner 83361*	*n* = 90	4*x*	Wagner & Wagner 1986
B. pinnatum St. John	WA: Skamania Co., *Wagner 63111*	*n* = 90	4*x*	Wagner in Fabbri 1963
B. pseudopinnatum W. H. Wagner	ON: Thunder Bay Dist., *Drife* in 1989	*n* = 135	6*x*	Wagner & Wagner 1990b
B. pumicola Coville	OR: Klamath Co., *R. M. Brown* in 1954	*n* = 45	2*x*	Wagner 1955
B. simplex E. Hitchc.	MI:Washtenaw Co., *Wagner 8142*	*n* = 45	2*x*	Wagner 1955
B. spathulatum W. H. Wagner	ON: Thunder Bay Dist., *Wagner 88036*	*n* = 90	4*x*	Wagner & Wagner 1990a
B. ×*watertonense* W. H. Wagner (*hesperium* × *paradoxum*)	AB: Waterton Lakes Natl. Park, *Wagner 83332*	2*n* = 180 (meiosis irreg.)	4*x*	Wagner et al. 1984

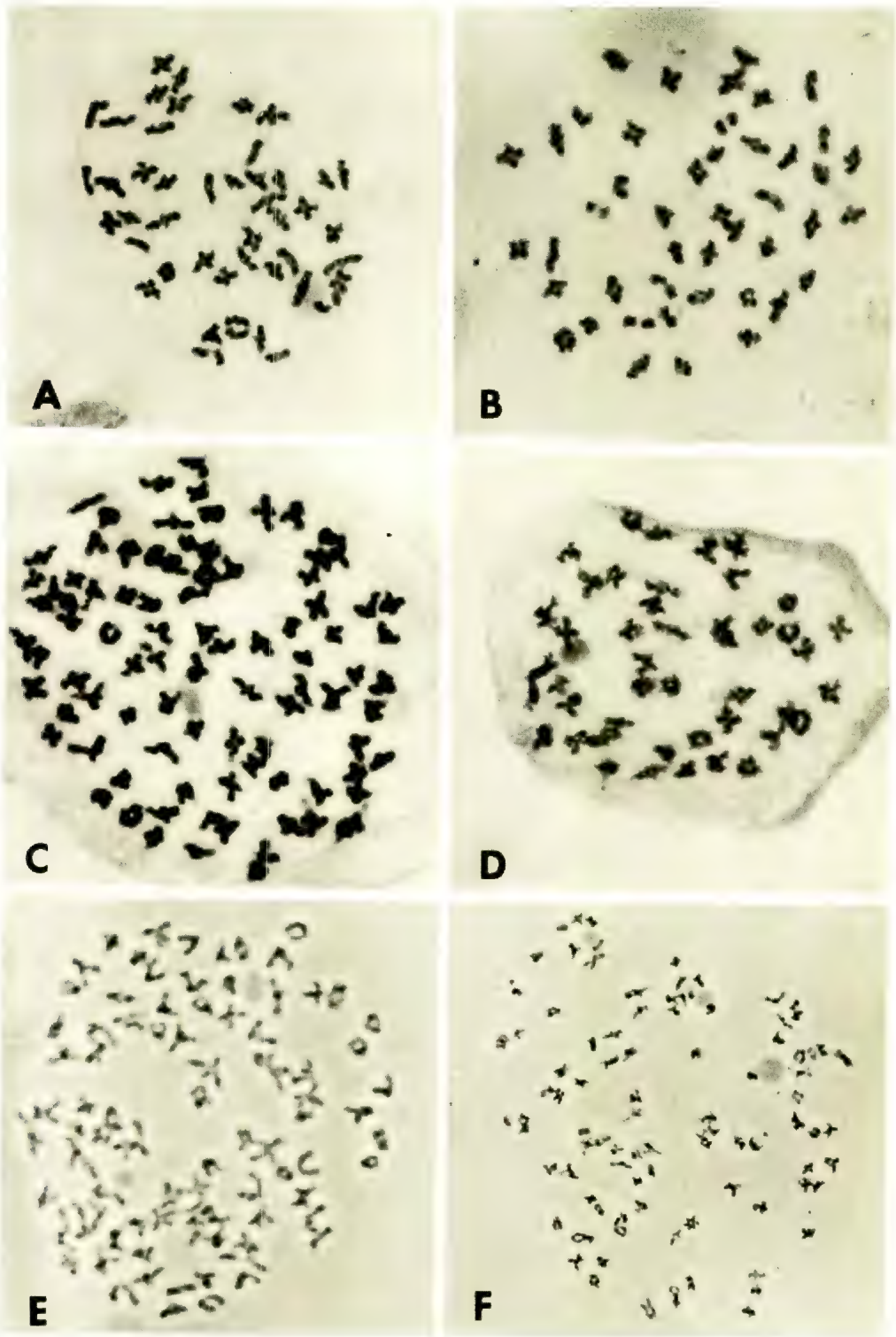

FIG. 1. Meiotic chromosomes of *Botrychium*; localities and voucher numbers are shown in Table 1. A. *Botrychium biternatum*, $n = 45$. B. *B. rugulosum*, $n = 45$. C. *B. jenmanii*, $n = 90$. D. *B. lunarioides*, $n = 45$. E. *B. echo*, $n = 90$. F. *B. ascendens*, $n = 90$.

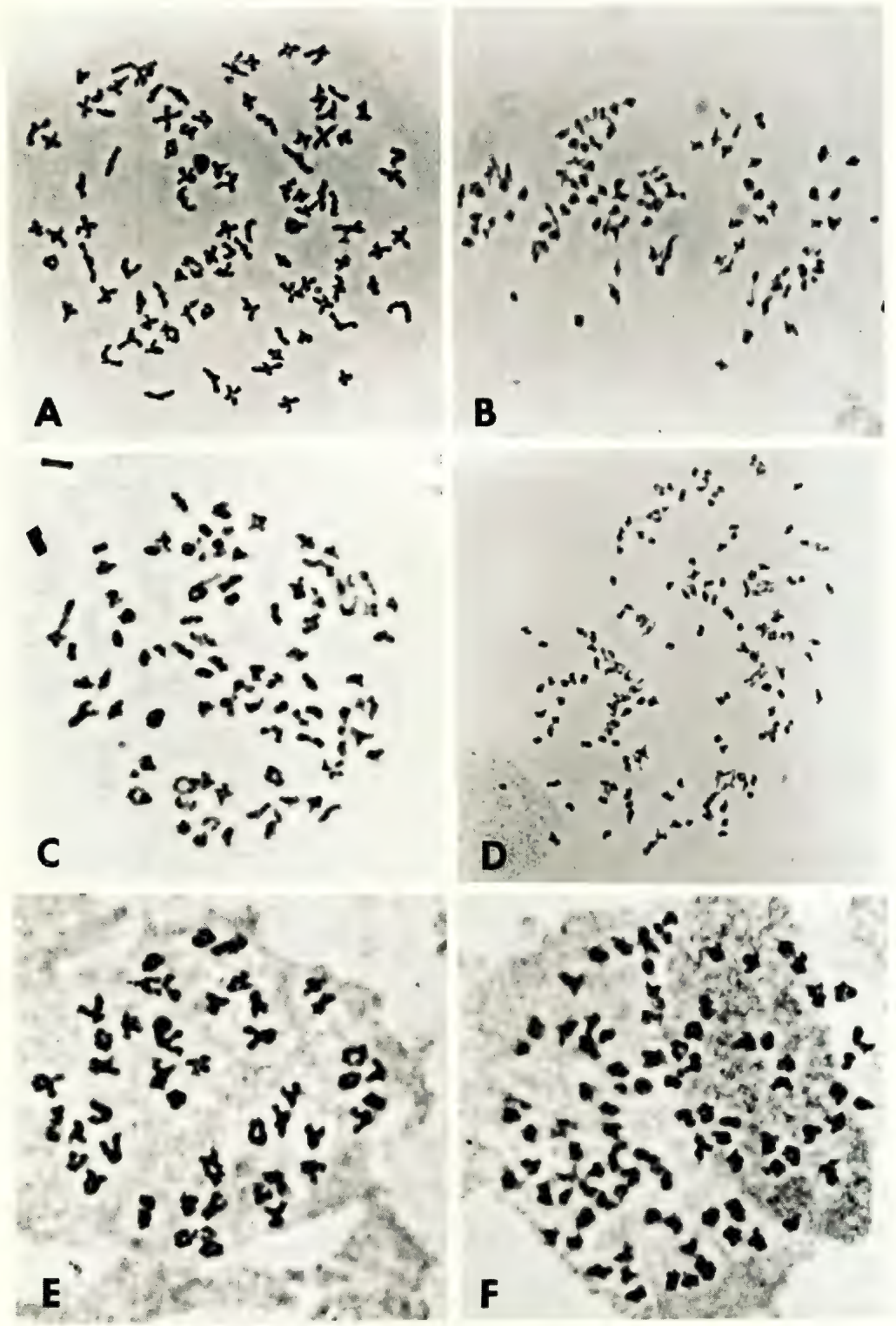

FIG. 2. Meiotic chromosomes of *Botrychium*; localities and voucher numbers are shown in Table 1. A. *Botrychium hesperium*, $n = 90$. B. *B. paradoxum*, $n = 90$. C. *B. pedunculosum*, $n = 90$. D. *B.* ×*watertonense*, ca. 41 II's, 99 I's. (Explanatory drawing in Fig. 4B). E. *B. lanceolatum* subsp. *lanceolatum*, $n = 45$. F. *B. pinnatum*, $n = 90$.

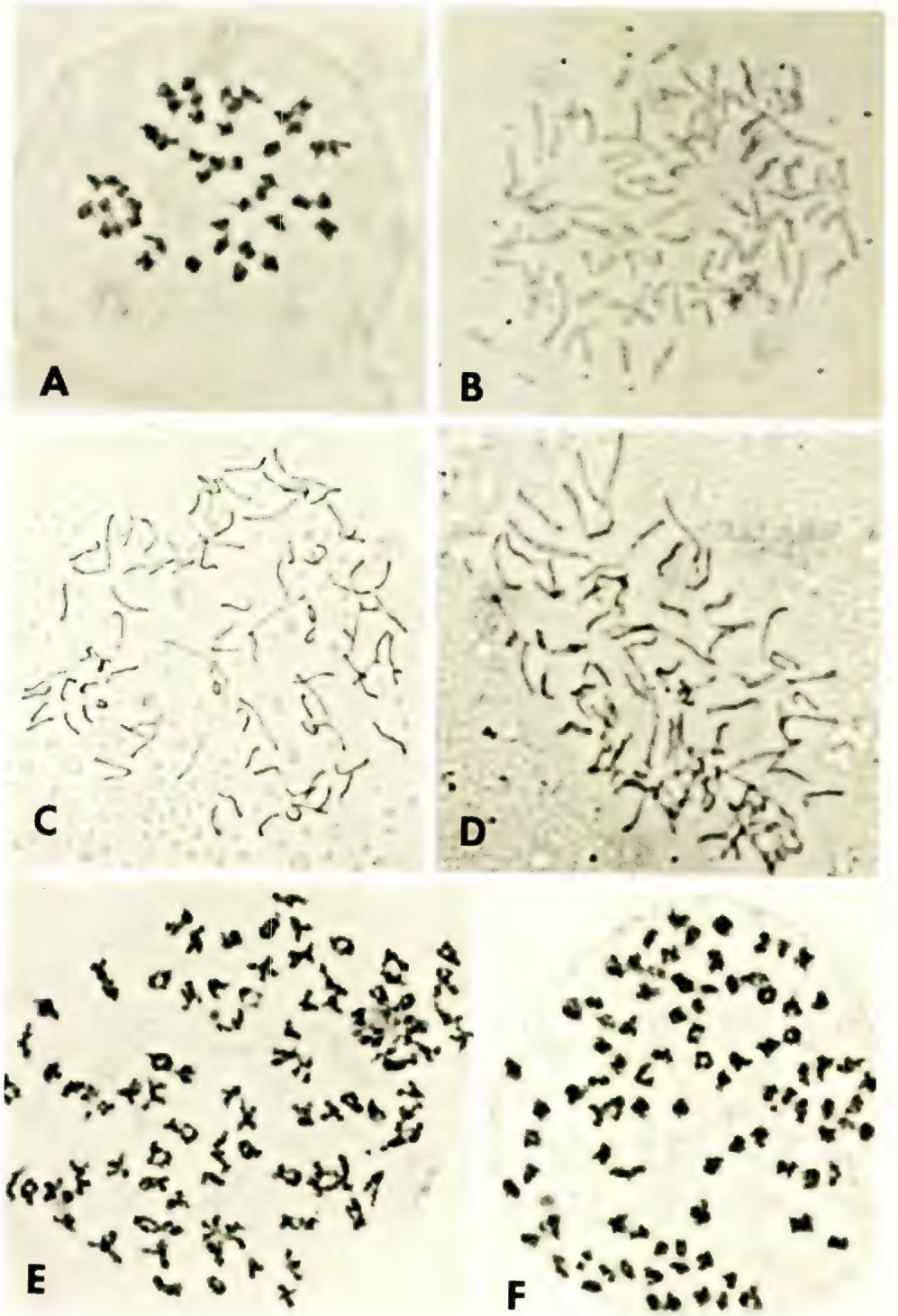

FIG. 3. Meiotic and somatic chromosomes of *Botrychium*; localities and voucher numbers are shown in Table 1. A. *Botrychium campestre*, $n = 45$. B. *B. mormo*, $2n = 90$. C. *B. pallidum*, $2n = 90$. D. *B. montanum*, $2n =$ ca. 90. E. *B. spathulatum*, $n = 90$. F. *B. acuminatum*, $n = 90$.

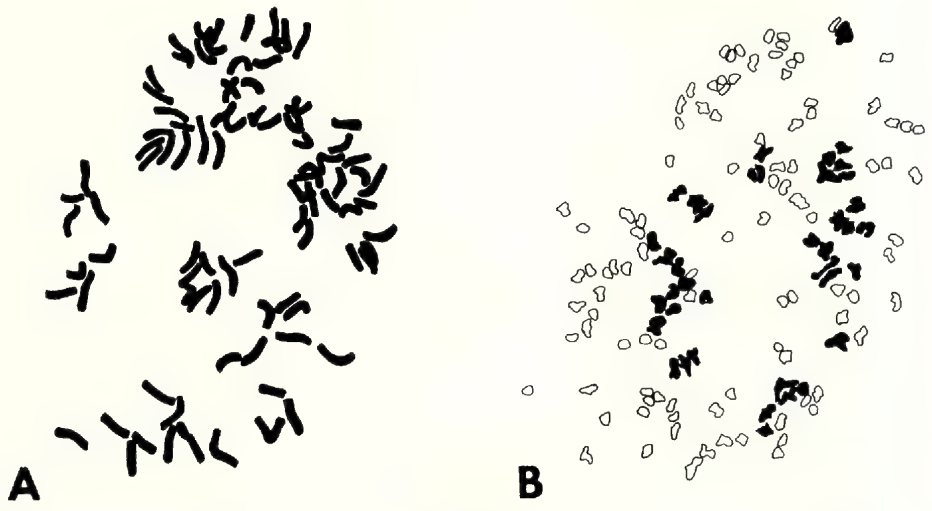

FIG. 4. A. Chromosomes of *Botrychium crenulatum*, $2n = 90$; locality and voucher number are shown in Table 1. B. Explanatory drawing of Fig. 2D, chromosomes of *B.* ×*watertonense*, ca. 44 II's and 99 I's.

The three subgenera of *Botrychium* in North America are *Osmundopteris*, *Sceptridium*, and *Botrychium*. (A fourth subgenus, *Japanobotrychium*, occurs in the Old World tropics.)

Subgenus *Osmundopteris*: *Botrychium virginianum* (L.) Sw., the most familiar and one of the most widespread species in the genus, occurs in Asia, Europe, North America, and extends as a morphological cline into South America. The chromosome number is tetraploid, with $n = 92$ ($x = 46$), an unusual base number, the only one in a genus in which almost all of the numbers are based on $x = 45$. The other member of subg. *Osmundopteris*, *B. strictum* L. Underw., from eastern Asia, also has an aberrant number, $n = 44$ (Sahashi 1982).

Subgenus *Sceptridium*: The evergreen grapeferns number approximately 25 species, seven of which occur in North America. Six of these are diploid with a chromosome number of $n = 45$. The seventh, *Botrychium jenmanii* L. Underw. (syn. *B. alabamense* Maxon), is a tetraploid with $n = 90$, a presumed ancient allopolyploid hybrid of the diploid species, *B. biternatum* (Sav.) L. Underw. and *B. lunarioides* (Michx.) Sw. (Wagner 1963). It occurs also in the Caribbean and Central America. No other potential hybrids are known in the North American members of the subgenus. There is, however, an undescribed taxon of *Sceptridium* in Kentucky and Tennessee, whose chromosome number and ploidal level are as yet undetermined.

Subgenus *Botrychium*: All 23 taxa of the moonworts have chromosome numbers based on 45. Surprisingly, half of the members of the subgenus are tetraploids, and one is a hexaploid. Until fairly recently only five taxa of moonworts were known in eastern North America, *B. simplex* E. Hitchc., *B. lunaria* (L.) Sw., *B. lanceolatum* (Gmel.) Angstr. (subsp. *angustisegmentum* (Pease & Moore) Clausen), *B. matricariifolium* A. Br., and *B. minganense* Victorin, and three in the West, *B. lanceolatum* (subsp. *lanceolatum*), *B. pumicola* Coville, and *B. pinnatum* St. John (formerly confused with *B. boreale* Milde of the Old World). Many of the 16 new species were simply overlooked or thought to be forms of the more common

TABLE 2. Sterile hybrid botrychiums in North America.

Species	Locality	Reference
B. ascendens × *crenulatum*	OR: Wallowa Co. *Wagner 83363a*	Wagner & Wagner 1986
B. echo × *minganense*	AZ: Apache Co. *Wagner 82104*	Wagner & Wagner 1983
B. lanceolatum × *minganense*	CO: Gunnison Co. *Wagner 82121*	Wagner & Wagner 1988
B. lanceolatum ssp. *angustisegmentum* × *matricariifolium*	MI: Alger Co. *D. Henson 2300*	Wagner & Wagner 1988
B. lunaria × *pinnatum*	BC: Bryan Boru Ck. *J. W. Easton* (UBC)	(Unreported)
B. lunaria × *simplex*	MI: Delta Co. *R. B. Wilson* in 1964	Wagner & Wagner 1988
B. lunaria × *spathulatum*	ON: Thunder Bay Dist. *Wagner 87237*	Wagner & Wagner 1988
B. matricariifolium × *minganense*	MI: Schoolcraft Co. *Wagner 81045*	Wagner & Wagner 1988
B. matricariifolium × *simplex*	MI: Midland Co. *Wagner 8997*	Wagner 1980, 1991
B. pedunculosum × *pinnatum*	OR: Wallowa Co. *Wagner 83361*	Wagner & Wagner 1986
B. ×*watertonense* W. H. Wagner (*hesperium* × *paradoxum*)	AB: Waterton Lakes Natl. Park *Wagner 83332*	Wagner et al. 1984

species, usually *B. lunaria* or *B. maticariifolium*. One of the helpful elements in recognizing the distinction of the new species has been the ploidal level, emphasizing the differences, for example, between *B. lunaria*, 2*x*, and *B. minganense*, 4*x*, and between *B. matricariifolium*, 4*x*, and *B. pseudopinnatum* W. H. Wagner, 6*x*.

Although for many years, authors believed that interspecific hybridization does not occur in these plants, we have much evidence now that it does (Wagner et al. 1985). Indeed, we have now encountered ten different widely scattered and sporadic types that appear to be intermediate between well-known species and that possess abortive spores. These are listed in Table 2. We have very little evidence of their chromosome behavior; however, the misshapen and highly variable spores, often very large and spherical among many small and shriveled ones, present strong evidence that meiosis is irregular.

Hybrids in *Botrychium* are rare, however; usually only a single plant is found among hundreds. These have more often been recognized only after large collections have been made and sorted, when they stand out as morphologically intermediate and difficult to assign to known species. So far we have identified only a

TABLE 3. Hypothetical parents for polyploid botrychiums.

Hypothetical parents (All orthospecies except *B. pinnatum*)	Presumed nothospecies
B. biternatum × *lunarioides*	*B. jenmanii*
B. campestre × *lanceolatum*	*B. echo*
B. campestre × *lunaria*	*B. spathulatum*
B. campestre × *simplex*	*B. gallicomontanum*
B. crenulatum × *montanum*	*B. ascendens*
B. lanceolatum × *lunaria*	*B. pinnatum*
B. lanceolatum × *montanum*	*B. pedunculosum*
B. lanceolatum × *pallidum*	*B. matricariifolium* —> *B. acuminatum* (metaspecies)
B. lanceolatum × *simplex*	*B. hesperium*
B. lunaria × *pallidum*	*B. minganense*
B. pinnatum × *simplex*	*B. pseudopinnatum*

few hybrids in the field and, with one exception, we have not succeeded in obtaining meiotic material of hybrids for chromosome study. In order to do so the putative hybrids must be identified as mature plants in the field, well past meiotic stages of sporogenesis, and tagged in the hope they will reappear the following spring, or the clump collected and overwintered as described above. The one exception is *Botrychium* ×*watertonense* W. H. Wagner, the hybrid between *B. hesperium* (Maxon & Clausen) W. H. Wagner & Lellinger and *B. paradoxum* W. H. Wagner, discussed in detail in Wagner et al. 1984. Meiotic counts of *B.* ×*watertonense* were obtained by the latter method. Meiosis proved to be irregular with the number of pairs of chromosomes ranging from 36 to 41 and the number of unpaired chromosomes from 99 to 110, the totals being approximately 180 chromosomes.

The major question involving the polyploids in *Botrychium* is whether they are autopolyploids from single pre-existing divergent species (orthospecies), or allopolyploids of interspecific hybrids (nothospecies). The first author to suggest that a species of moonwort was actually a polyploid hybrid was Meyer (1981). He proposed that *B. matricariifolium* originated as the sterile hybrid of *B. lanceolatum* and *B. lunaria* (1981, pp. 613 ff., figs. 2, 3). His hypothesis, however, is unlikely, because a number of morphological characters do not conform to this interpretation.

Using such characters as (1) trophophore blade cutting and (2) shape; (3) relative development of the basal pinna pair; (4) marginal denticulation; (5) venation pattern; (6) epicuticular wax; (7) relative length of sporophore; and (8) pinnation of sporophore, origins of some of the polyploid taxa can be hypothesized. For some of the polyploids there are no obvious candidates as possible parents. One of these is *B. acuminatum* W. H. Wagner, a rare species of the Lake Superior region. It is very close morphologically in most characters to *B. matricariifolium*, with which it co-occurs. *Botrychium acuminatum* may represent an example of metaspeciation in which divergent evolution has taken place from an allopolyploid nothospecies, in this case, *B. matricariifolium*.

The most remarkable polyploid is *B. paradoxum* W. H. Wagner, which differs from all other known species, diploid or polyploid, and for which there are no known relatives or postulated parental combinations.

Hypotheses of reticulate origin for the various polyploid taxa are listed in Table 3. They are presented here in the hope that they will be tested in various ways, including observations on chromosome pairing behavior in natural backcrosses, comparisons of isozyme patterns of the postulated parents and their allopolyploid presumed descendants, and observations on chloroplast DNA. Also theoretically at least, it should be possible to reproduce the proposed hybridizations experimentally.

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VERBESINA PELLUCIDA (ASTERACEAE-HELIANTHEAE), A NEW SPECIES FROM THE ISTHMUS OF TEHUANTEPEC, OAXACA, MEXICO

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Collecting efforts in the District of Tehuantepec, Oaxaca, Mexico, have resulted in the discovery of a new species of *Verbesina*. The species is described and illustrated, and its affinities to other verbesinas of the region are discussed.

Verbesina pellucida Villaseñor & Panero, sp. nov.—TYPE: MEXICO. Oaxaca: Km 10 of the rd to Santa María Chimalapa, ca. 10 km E of the intersection of this rd and the rd Palomares-Matías Romero, 400 m, 17 Feb 1992, *Panero & Campos 2746* (holotype: MEXU!; isotypes: K! MA! MICH! MY! QCA! SI! TENN! TEX! UC! US! 7 additional isotypes to be distributed by MEXU). Fig. 1.

A *V. auriculata* capitulis majoribus, foliis sessilibus oblanceolatis, et phyllariis exterioribus herbaceis suborbicularibus differt.

Small shrubs 0.4–0.8 m tall; stems terete, herbaceous parts somewhat succulent, puberulent, stramineous or beige, woody parts glabrous and dark brown. Leaves alternate, pinnately veined, apparently readily deciduous and only the uppermost present at anthesis; blades 2.8–14.1 cm long, 1.4–4.6 cm wide, somewhat smaller distally towards the capitulescence, oblanceolate to oblong, adaxial surface glabrous, bluish green, abaxial surface glabrous and creamy green, central vein glabrous, stramineous, raised and conspicuously outlined against green background, higher-order veins forming a pellucid reticulum visible with the unaided eye, margins crenate, apex acuminate to acute, rarely obtuse, base attenuate. Capitulescence of 1–3 heads, solitary or simple dichasia; peduncles (2–) 5–9 cm long, puberulent, stramineous or beige. Heads heterogamous, radiate, hemispheric, 0.8–1.2 cm high 1.0–1.5 cm wide (excluding ligules); receptacle 0.5–0.7 cm wide, flat to slightly convex. Phyllaries 17–22 in 2–3 subequal series; phyllaries of first series 0.8–1.2 cm long, 4–5 mm wide, appressed, herbaceous, foliiform, oblong to suborbicular, sparsely puberulent, green with a conspicuous reticulate venation, margins sparsely ciliate; phyllaries of second series 7–9 mm long, 1.5–2.0 mm wide, appressed, herbaceous, chartaceous, oblanceolate, resembling pales, glabrous to sparsely puberulent, stramineous green, margins sparsely ciliate or glabrous. Pales 7–8 mm long, ca. 2.5 mm wide, obovate to oblanceolate, shallowly

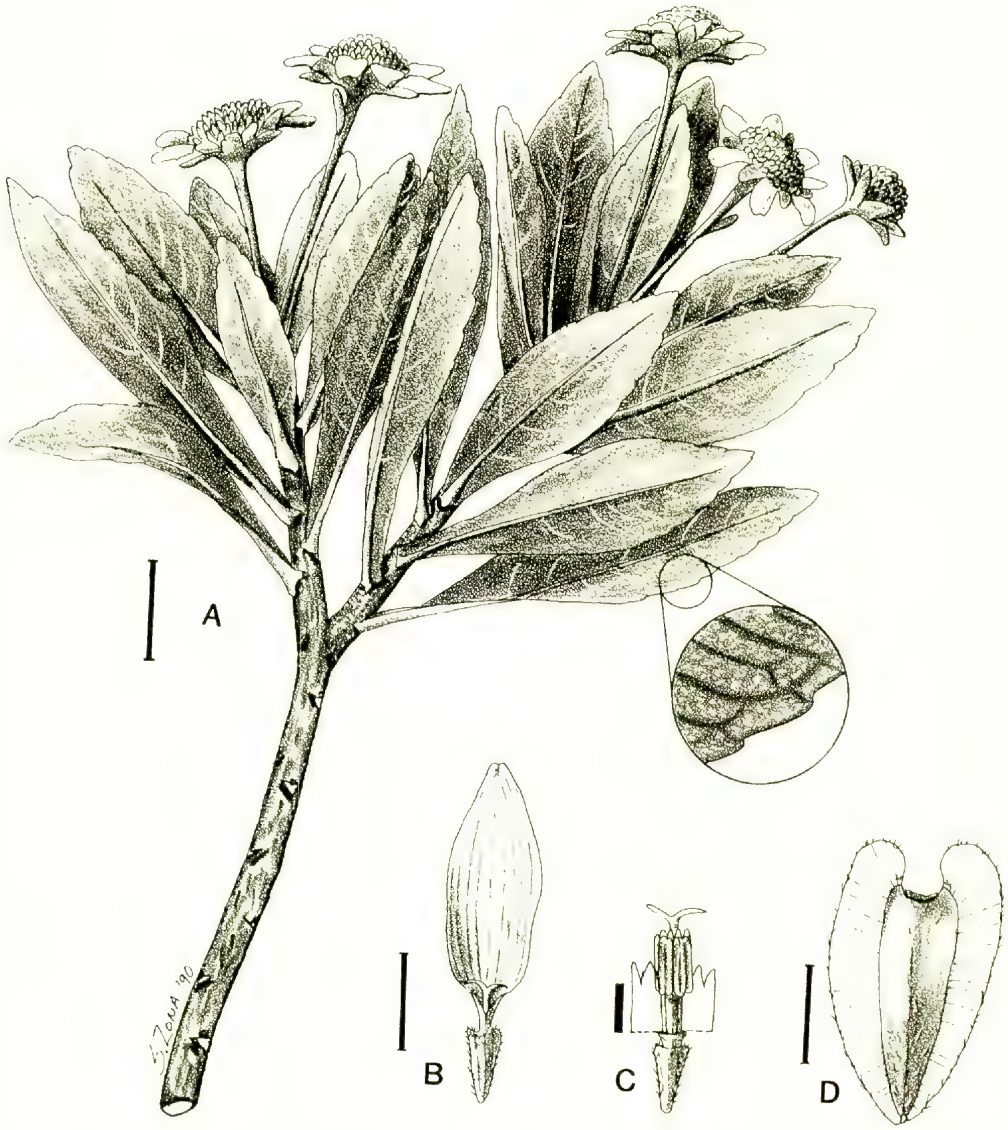

FIG. 1. *Verbesina pellucida* (*Cedillo 1121*). a. Flowering branch. b. Ray flower. c. Disk flower. d. Disk achene. (a, bar = 1.5 cm; b, bar = 5 mm; c, bar = 4 mm; d, bar = 2 mm.)

conduplicate, conspicuously concave distally, sparsely puberulent or glabrous, stramineous-green, apex acute to acuminate. Ray flowers 13–17, corollas golden-yellow, pistillate; ligules 1.1–1.3 cm long, ca. 5 mm wide, ovate to oblong, sparsely puberulent on veins of abaxial surface, apex trifid; tube ca. 1.5 mm long, moderately puberulent. Ray achene (immature) ca. 5 mm long, 2.5 mm wide, oblanceolate to oblong, sparsely sericeous, shiny black, wings sparsely ciliate, stramineous or yellowish green; pappus none. Disk flowers (150–) 170–200 (–220), corollas golden-yellow, hermaphrodite; throat ca. 4 mm long, narrowly campanulate to tubular, sparsely puberulent, especially on base; tube 1.0–1.2 mm long, glabrous to sparsely puberulent; lobes 0.5–0.8 mm long; anthers ca. 2 mm long, black, appendages ca. 0.2 mm long, stramineous; styles 4.0–4.5 mm long, style branches 1 mm long, acute. Disk achenes resembling ray achenes, sparsely sericeous. Chromosome number: n = 17.

Verbesina pellucida resembles *V. auriculata* DC. in several noteworthy features. The two species have oblanceolate, concave pales (also seen in the related *V. abscondita* Klatt), stramineous or beige, succulent stems, and a tendency to have entirely winged petioles. *Verbesina pellucida* can be readily separated from *V. auriculata* by differences in the involucre and capitulescence. *Verbesina pellucida* has an involucre of subequal phyllaries; the phyllaries of the outermost series are herbaceous, foliiform, and suborbicular. In V. *auriculata,* the involucre is graduated, and the phyllaries of the outermost series are lanceolate to narrowly lanceolate, indurate at base, and have reflexed herbaceous apices. The capitulescence of *V. pellucida* is distinctive in that the heads are borne on relatively long peduncles and are solitary or arranged in simple dichasia, whereas in *V. auriculata* and *V. abscondita* the heads are arranged in monochasial thyrsoid capitulescences. The new species, because of its conspicuously large heads, could be confused with the parapatric *V. sousae* and *V. oaxacana*; however, it can be easily separated from them by its sessile, oblanceolate leaves and herbaceous involucre.

The specific epithet is derived from the conspicuous pellucid reticulum formed by the higher order veins.

Additional Specimens Examined. **Mexico.** Oaxaca: Distrito de Juchitán, Mpio. de Asunción Ixtaltepec, 5 km al W de Santiago Ixtaltepec, por la carr. a Santa María Chimalapa, 29 Aug 1991, *Campos 3878* (MEXU); Distrito de Juchitán, Mpio. de Santa María Guienagati, 11 km al NW of Lachiviza, por el camino a Lachiguiri, 15 Mar 1986, *Tenorio 11121, Torres & Martínez* (CHAPA, MEXU); Distrito de Juchitán, Mpio. de Asunción Ixtaltepec, 8 km al NW de Santiago Ixtaltepec, 200 m, 23 Feb 1982, *Cedillo 1121* (ENCB, MEXU, RSA).

ACKNOWLEDGMENTS

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REVISION OF CAREX SECTION OVALES (CYPERACEAE) IN MEXICO

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INTRODUCTION

Carex L. section *Ovales* Kunth (subgenus *Vignea* P. Beauv. ex T. Lestib.) is the largest and most difficult section of the genus in the New World. Upwards of 75 species have been recognized in North America, including Mexico (Mackenzie 1931; Hermann 1970, 1974). It is largely confined to the New World, with only 5 species native in temperate Eurasia, *C. bohemica* Schreb., *C. maackii* Maxim., *C. macloviana* d'Urv., *C. ovalis* Gooden., and *C. pachystachya* Steud. (including *C. pyrophila* Gand.). Three of these, *C. macloviana*, *C. ovalis*, and *C. pachystachya*, are also native in North America. The western North American *C. subfusca* W. Boott is native in Hawaii. Otherwise, all occurrences of section *Ovales* in the Old World are introductions, including several species in New Zealand, and the weedy *C. longii* Mack. introduced in Hawaii (and New Zealand). The section, one of the most widespread in the New World, is distributed from the Arctic to Patagonia, although the greatest diversity of species occurs in the mountains of the western United States.

The section is considered very difficult taxonomically, and treatments of local areas vary considerably in the number of species recognized. Statements such as "...there is a strong temptation to recognize fewer species" (Voss 1972) are frequent in floristic literature. Working with the section, however, suggests that a significant component of the taxonomic difficulty within the group is the large number of species that look rather similar, at least on herbarium sheets, and that are distinguished by small differences. Extensive intergradation between recognized species and consequent blurring of species limits does not seem to be as pervasive as some literature would suggest, though certainly there are a number of problem species and species aggregates. Gaps between species may be narrow, but often they are deep. As well, the large number of species in the section, and the fact that it has not proven possible to subdivide it easily into discreet, small, natural groups, have discouraged people from tackling it, and there has been no overview of the entire section since Mackenzie (1931).

Essentially nothing is known about the reproductive biology of Mexican members of section *Ovales*. Studies on some members of the *Carex macloviana* aggregate northward (Whitkus 1988) found that the species are self-compatible and likely autogamous in the wild. Apomixis was not found by Whitkus (1988) and has never been conclusively demonstrated in any species of *Carex*. Only one chromosome number based on Mexican material is known, $n = 37$ in *C. peucophila* (Beaman et al. 1962), although a few other species have been counted from Canada or the United States.

This treatment represents a considerable amplification on past treatments of the section in Mexico. Liebmann (1850) and Kükenthal (1909) reported 3 species, *Carex longii* (as *C. leporina* var. *bracteata* Liebm. and *C. albolutescens* Schwein., respectively), *C. orizabae* Liebm. (as *C. macloviana* in Kükenthal, 1909), and *C. peucophila* T. Holm (as *C. pinetorum* Liebm.). Mackenzie (1931) reported only 4 species, *C. bonplandii* Kunth, *C. festivella* Mack., *C. longii*, and *C. peucophila*. Hermann (1974), in the first comprehensive treatment of Mexican species of *Carex* since Liebmann's, reported 13 species, but with only brief descriptions and generalized range statements. One of the 13, *C. purdiei* Boott, was reported only doubtfully and was deleted from the Mexican flora by Reznicek (1990).

Subsequent to Hermann's (1974) treatment, many new collections have accumulated. In reviewing this new material, particular attention was paid to the possible identity of Mexican collections with United States species, especially those from the western cordillera, as well as Central and South American species. This treatment recognizes 14 species; however, only 6 names remain in common with Hermann's treatment. Of the 14 species recognized here, 6 are widespread, being known from 5 or more collections over at least several states (*C. curviculmis* Reznicek, *C. lagunensis* M. E. Jones, *C. longii*, *C. microptera* Mack., *C. orizabae*, and *C. peucophila*). *Carex subfusca* is frequent locally, but confined to Baja California Norte. Four species, *C. athrostachya* Olney, *C. brevior* (Dewey) Mack., *C. tribuloides* Wahlenb., and *C. wootonii* Mack., are widespread northward, but have been collected only 1–3 times in Mexico, and three species, *C. festivelloides* Reznicek, *C. tolucensis* (F. J. Herm.) Reznicek, and *C. interjecta* Reznicek, are apparently rare Mexican endemics known thus far only from their types. Considering the number of species known from very few collections, this treatment must still be considered preliminary.

All the Mexican members of section *Ovales* are montane plants; essentially none occur below 1000 m, and most species are confined to above 2000 m. Most are plants of open, moist meadows, and may very locally even be important components of such habitats. A few occur in denser shade of forests. Although found essentially throughout Mexico, the diversity of species is greatest in the Transvolcanic Belt, in the Distrito Federal, and the State of México. There, species occurring primarily in the Sierra Madre Occidental, such as *C. lagunensis* and *C. microptera*, co-occur with species occurring mostly in the Sierra Madre Oriental, such as *C. peucophila* or *C. longii*. Most of the local endemics also occur in the Transvolcanic Belt.

Mexican members of section *Ovales* are in no way a natural group; the closest relatives of most of the Mexican species, even the endemics, are probably extralimital species. Of the 14 species here recognized; 7 are endemic to Mexico or nearly so (*Carex peucophila* and *C. orizabae* barely range into Guatemala); 4 species (*C. athrostachya*, *C. microptera*, *C. subfusca*, and *C. wootonii*) are plants of the western Cordillera of the United States that range south as far as Mexico; 2 species (*C. longii* and *C. tribuloides*) are common eastern North American species disjunct to Mexico, of which one, *C. longii*, also ranges south through the Caribbean and Central America to Ecuador; and *C. brevior* is transcontinental in North America.

Mackenzie (1931) divided the section into 11 unranked groups based on perigynium and scale features, characteristics of the vegetative shoots including sheath morphology, texture, and color, and inflorescence bract length. To what extent these groups are natural is still unclear, and no attempt has been made here to

assign Mexican species to Mackenzie's groups. In fact, relationships within the section are too poorly known to speculate with much confidence about the phylogenetic relationships of the endemics, though most appear to be similar to species from the western United States.

The primary taxonomic characters that have proven useful in the systematics of the section reside in the perigynia, and include size, shape, color, beak/body proportions, marginal serrulations, and beak apices. Achenes, rhizomes, anthers, scale color, inflorescence morphology, and leaf and sheath characters also provide some useful features. As such, essentially mature, complete material is vital for determinations. Of particular importance for identification is understanding that perigynia can vary widely in shape from the bottom to the top of a spike. The lowermost perigynia in a spike are the widest, but are often unusually short and sometimes distorted and asymmetrical. The uppermost perigynia in a spike are the narrowest and tend to be essentially similar in shape among all the species. Thus, the lower (but not the lowermost one or two) to middle perigynia in a spike are most reliable when applying measurements from the key. As well, all plants that normally have large or wide perigynia occasionally produce depauperate spikes or inflorescences with perigynia smaller and often narrower than typical for the species. Before keying plants, sampling of the collection to find the largest undistorted, ± symmetrical perigynia (excepting sometimes the lowermost in a spike) is extremely helpful. Perigynium width in the keys and descriptions has been measured with the wings flattened out, but in some species the wings apparently arch forward in life, as shown in the illustrations. Colors of perigynia and scales also provide important features for identification in some instances; however, both scale and perigynium colors may be unusually pale on plants growing in dense shade, and may fade with weathering and with age on herbarium specimens.

An additional complication with species occurring in alpine sites is that at higher elevations and in exposed situations, all tend to become dwarfed and compact. The different species thus may look remarkably similar. These plants can be exceptionally difficult to determine reliably.

Most keys to the section (e.g., Hermann 1970, 1974) are very difficult to use, because major, early subdivisions in the keys often rely on whether or not the ultimate apex of the beak is flattened and serrulate or terete and smooth and on whether or not the perigynia are planoconvex or flattened and scalelike. These distinctions are rather subtle, and their interpretation requires substantial – some might say transcendental – familiarity with the section. The key presented here avoids these features, except as subsidiary characters for distinguishing species pairs, and, I hope, will be easier to use.

Immature specimens, with barely developed perigynia, can sometimes be recognized, if complete, but cannot be keyed. Slightly immature material can sometimes be keyed by applying the following facts. Perigynia mature basipetally, thus beaks are essentially full size before the body is fully developed, especially in species with broadly winged perigynia. With experience, rough estimates of size and shape of perigynia can be made from immature material based on the size and width of the beak and comparison with reliably determined material. Nerves on the perigynia also tend to be very faint until full maturity, even among species with distinctly nerved perigynia. Scale color develops fully before anthesis, but perigynium color (if not green) develops only near or at maturity.

All names based on Mexican specimens are typified here. Names of all taxa recognized are also typified, if possible, even if the types are extralimital, but

synonymy based on types from beyond Mexico is not given. However, because there exists considerable confusion about their application, all names of Latin American members of section *Ovales* from beyond Mexico that are mentioned in the text are typified, even if they are not treated in detail. Species are arranged alphabetically, and all Mexican specimens that were examined are cited, arranged alphabetically by states and by collector and number.

TAXONOMY

Carex section **Ovales** Kunth, Enum. Pl. 2: 394. 1837.—TYPE: *Carex ovalis* Gooden. [*Carex leporina* of authors, not L.]

Cespitose to occasionally mat-forming perennials, rhizomes very short to ± elongate and short-creeping; culms trigonous, bladeless basal sheaths always present, but sometimes rapidly disintegrating. Leaves usually 3–10 on the fertile culms, mostly on the lower 1/10–1/3 of the culm, occasionally the culm more leafy. Vegetative culms present, sometimes much leafier than the fertile culms and with the leaves strongly tristichous. Inflorescences densely capitate with the spikes essentially indistinguishable to open and elongate with at least the lower spikes clearly separated, 0.6–10 cm long, the lower inflorescence bracts usually scalelike or at most setaceous-prolonged, shorter than the inflorescence, rarely leafy and much longer than the inflorescence; spikes single at the nodes, gynaecandrous, lance-ovoid to obovoid or turbinate, sometimes with a prominent staminate basal portion (especially on the terminal spike). Perigynia with bodies narrowly lanceolate to orbicular or even reniform, strongly flattened, scalelike, biconvex, or planoconvex, essentially lacking internal spongy tissue, narrowly to broadly winged and serrulate-margined, at least above, gradually tapered to abruptly contracted to a beak; beaks flattened and serrulate-margined except sometimes at the apex. Achenes biconvex, narrowly ovate to oblong to obovate. Chromosome numbers (Whitkus 1991): $n = 26–45$.

KEY TO CAREX SECTION OVALES IN MEXICO

1. Inner band of especially the upper leaf sheaths herbaceous and green nearly to apex; pistillate scales whitish hyaline, green, or pale silvery brown.
   2. Perigynia 1.6–2.8 mm wide, (1.3–) 1.6–2.2 times as long as wide; widest leaves 2–4 (–4.5) mm wide. 7. *C. longii.*
   2. Perigynia 0.9–1.5 (–1.7) mm wide; (2.3–) 2.7–4 (–5) times as long as wide; widest leaves (3.5–) 4–5.5 (–7) mm wide. 13. *C. tribuloides.*
1. Inner band of leaf sheaths hyaline, whitish to pale brown for most of their length; pistillate scales yellowish brown to purplish black.
   3. Larger perigynia 2–3.4 mm wide; usually 1.1–2.2 times as long as wide (except often in *C. wootonii*).
      4. Larger perigynia 5.5–7.5 mm long, (2–) 2.2–3.1 times as long as wide. 14. *C. wootonii.*
      4. Larger perigynia 3.2–5.4 mm long, usually 1.1–2.2 times as long as wide.
         5. Terminal spikes with a prominent staminate portion 3–9 (–14) mm long; larger perigynia 2.4–3.4 mm wide; inflorescences usually elongate, (1.3–) 2.5–6.5 cm long. 2. *C. brevior.*
         5. Terminal spikes with the basal staminate portion inconspicuous, 1–3 mm long; larger perigynia 2–2.6 (–2.8) mm wide; inflorescences capitate to ovoid, (0.8–) 1.2–2.5 (–3.5) cm long.
            6. Perigynium bodies usually (1.9–) 2.5–4 (–5.4) times the length of the beaks; beaks 0.6–1.2 (–1.5) mm long, usually flattened and serrulate-margined nearly to apex.

7. Larger anthers 1.8–2.8 mm long; larger perigynia 4.3–5.4 mm long; spikes usually 4–8; plants densely cespitose. 6. *C. lagunensis.*
7. Larger anthers 1.2–1.8 mm long; larger perigynia 3.5–4.4 (–4.7) mm long; spikes usually 2–5; plants usually with short-creeping rhizomes. 10. *C. peucophila.*

6. Perigynium bodies usually 1.9–2.4 times the length of the beaks; beaks 1.3–1.6 mm long, the apical 0.4–0.6 mm terete and smooth. 12. *C. tolucensis.*

3. Larger perigynia 1–1.9 mm wide, usually more than 2.2 times as long as wide.
8. Larger perigynia 2.5–3.5 (–4.5) times as long as wide, usually (3.0–) 3.8–5.8 mm long; beaks (0.8–) 1.2–1.9 (–2.1) mm long.
9. Lowermost inflorescence bracts consistently 1.2–6 (–9) cm long, exceeding the inflorescence.
10. Larger perigynia 3–4.6 mm long, 1–1.5 mm wide; achenes 1–1.6 mm long, 0.7–0.9 mm wide. 1. *C. athrostachya.*
10. Larger perigynia 4.3–5.8 mm long, usually 1.5–1.9 mm wide; achenes 1.7–2 mm long, 1–1.3 mm wide. 4. *C. festivelloides.*
9. Lowermost inflorescence bracts usually scalelike and shorter than the inflorescence, occasionally but not consistently setaceous-prolonged to 1.6 (–8) cm long.
11. Perigynia dark reddish brown to purplish black on the beak and usually the distal portion of the body, the same color as the pistillate scales and thus inconspicuous in the uniformly dark inflorescence, usually clearly 1–6-nerved over achene adaxially, beaks usually 1.4–1.9 mm long. 9. *C. orizabae.*
11. Perigynia green to pale brown distally except for a narrow, darker stripe on the beak and the beak apex, contrasting with the brown to reddish or purplish brown pistillate scales and thus forming a two-toned inflorescence; usually nerveless or sometimes faintly 1–5-nerved over achene adaxially; beaks usually 1–1.5 mm long.
12. Achenes (1.1–) 1.2–1.4 mm wide; plants loosely cespitose to colonial, rhizomes short-creeping. 3. *C. curviculmis.*
12. Achenes 0.8–1.1 mm wide; plants densely cespitose, rhizomes very short. 8. *C. microptera.*

8. Larger perigynia 1.3–2.6 times as long as wide, usually 2.7–4.5 mm long; beaks 0.6–1.5 mm long.
13. Pistillate scales uniformly dark reddish brown to purplish black; inflorescence densely capitate, the individual spikes not easily discernible. 9. *C. orizabae.*
13. Pistillate scales yellowish brown to reddish brown, with a greenish or paler midrib; inflorescences capitate-ovoid to ± elongate, the individual spikes usually clearly visible.
14. Achenes (1.1–) 1.2–1.5 mm wide; perigynia 1.6–1.9 mm wide; spikes 2–5 (–7); plants usually with short-creeping rhizomes. 10. *C. peucophila.*
14. Achenes 0.9–1.1 (–1.2) mm wide; perigynia 1.2–1.8 mm wide; spikes (3–) 5–9; plants cespitose.
15. Inflorescences elongate, 2.5–3.5 cm long, the lower spikes clearly separate; leaves on the lower 2/5–2/3 of the culm; perigynia appressed, (3.5–) 3.7–4.5 mm long. 5. *C. interjecta.*
15. Inflorescences capitate-ovoid, 1.1–2.2 (–2.8) cm long, the spikes discernible but overlapping; leaves on the lower 1/10–2/5 of the culm; perigynia spreading-ascending, 2.7–4.1 mm long. 11. *C. subfusca.*

1. Carex athrostachya Olney in A. Gray, Proc. Am. Acad. 7: 393. 1868.—TYPE: U.S.A. California: Yosemite Valley, 4000 ft, 17 Jun 1863, *Brewer 1650* (lectotype, here designated: GH!; isolectotype: MO!). Figs. 1a, 2a.

Densely cespitose in large clumps; fertile culms 15–80 cm tall, erect, trigonous, scabrous-angled; bladeless basal sheaths pale brown, disintegrating into short, dark brown fibers. Leaves 2–5, on the lower 1/5–1/3 of the culm; blades 3–30 cm long, 1.2–4 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 1.5–9 cm long, tightly enveloping culms, glabrous,

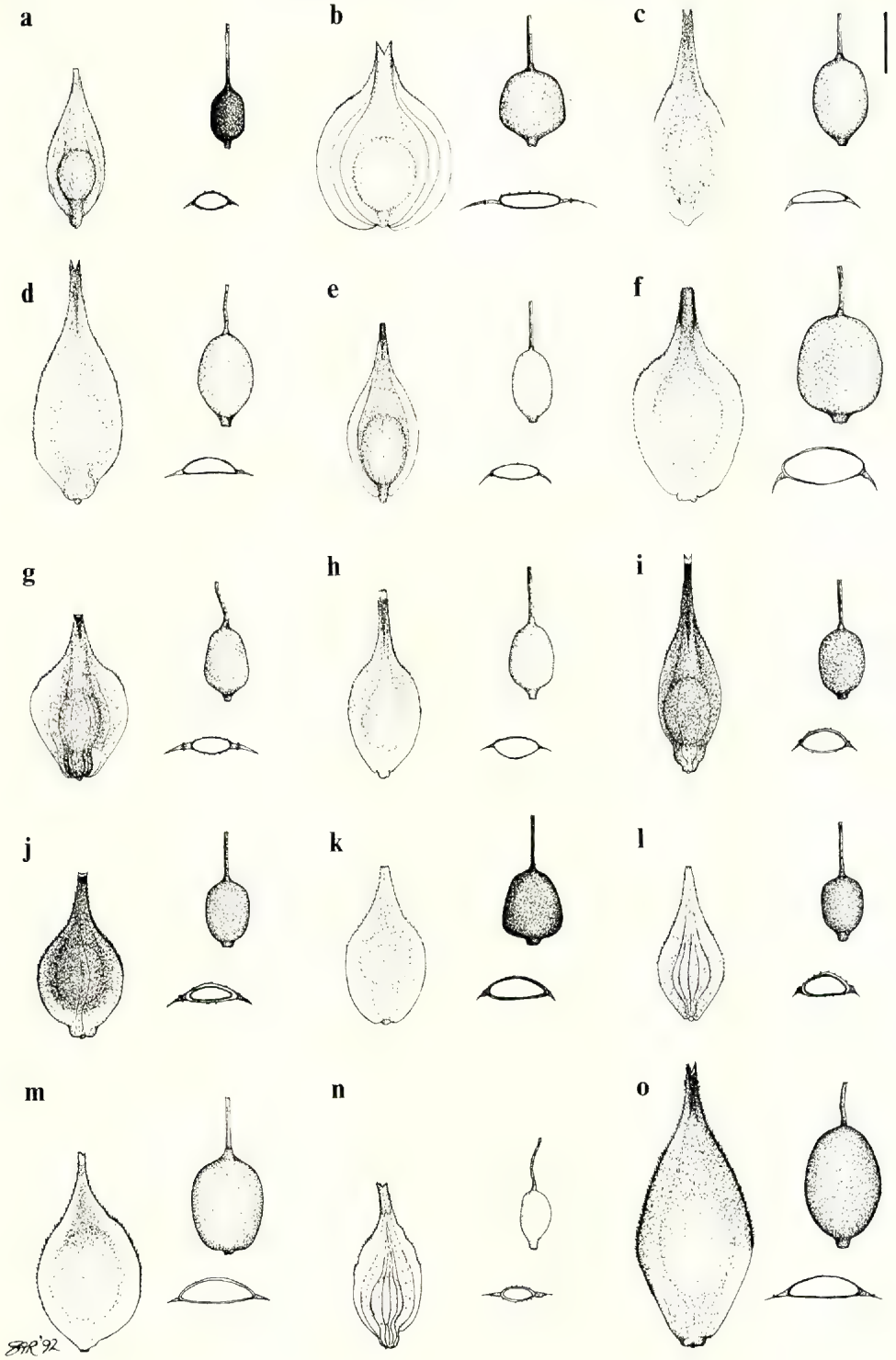
green; the inner band of sheaths glabrous, whitish hyaline, sometimes prolonged up to 4 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 1.5–6 mm long, rounded, the free portion entire to ± erose, up to ca. 1 mm long. Vegetative culms ca. 1–15 cm tall with ca. 5–9 leaves; leaves tristichous and mostly clustered in the upper 1/2 of the culm. Inflorescences 0.8–2.2 cm long capitate-ovoid, the spikes strongly overlapping and often barely distinguishable, spikes single at nodes, sessile, lowermost bracts setaceous to ± leafy, 1.2–9 cm long and up to ca. 2 mm wide, conspicuous, sheathless but dilated at base, the upper bracts much reduced; spikes 4–10, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, ca. 5–10 mm long, pistillate portion 4.5–9 mm long, 4.5–6.5 mm wide, ca. 10–40-flowered, staminate portion ca. 1–2 mm long, appressed against the pistillate portion, ca. 1–4-flowered. Pistillate scales 2.4–4.3 mm long, 0.9–1.3 mm wide, narrowly ovate, acute to acuminate, yellowish brown to dark reddish brown with a narrow green center and narrow hyaline margins, 1 (–3)-nerved. Staminate scales 1.9–4.5 mm long, 0.8–1.3 mm wide, lanceolate to narrowly ovate, acuminate, yellowish brown to dark reddish brown with a narrow green center and narrow hyaline margins, 1-nerved. Perigynia 3–4.6 mm long, 1–1.5 mm wide, 2.5–3.2 (–4.5) times as long as wide, ascending, biconvex and very thin except where distended by the achene, with narrowly ovate to narrowly elliptic bodies 1.9–3 mm long, 1.5–2.2 (–2.9) times as long as wide and 1.5–2.5 times as long as the beak, widest 0.9–1.5 mm above base, narrowly winged and serrulate-margined above the widest part, gradually tapered into an indistinct beak, green to pale brown, glabrous, sessile to short-stipitate, adaxial side nerveless or up to 6-nerved over achene, abaxial side faintly 3–9-nerved over achene; beaks 0.8–1.6 mm long, flattened and serrulate-margined but with the apical 0.4–0.6 mm terete and smooth, the apex bidentulate with irregular teeth up to 0.2 mm long. Achenes 1–1.6 mm long, 0.7–0.9 mm wide, 1.2–1.6 times as long as wide, biconvex, narrowly ovate-oblong, pale brown, short-stipitate; style straight; stigmas 2. Anthers 3, 1.1–2.2 mm long. Chromosome number: $n = 34$ (Packer & Whitkus 1982).

Known only from wet meadows and stream valleys in the Sierra San Pedro Mártir of Baja California Norte at about 2100 m elevation (Fig. 3). Collections made in late August were in fruit.

Specimens Examined. Baja California Norte: Sierra San Pedro Mártir, Santa Rosa, 30°48'N, 115°21'W, 20 Aug 1967, *Moran & Thorne 14389* (SD); La Grulla, 30°54'N, 115°27'W, 22 Aug 1967, *Moran & Thorne 14491* (RSA, SD).

Carex athrostachya is a very widely distributed western North American species ranging from Alaska to Saskatchewan and south to California and westernmost Texas. It is a species of transient or cyclical habitats at low to mid-montane elevations, including temporary ponds holding water only in spring, shores of rivers, lakes, and streams with fluctuating water levels, and early successional wet meadows. It probably has a long-lived seed bank.

FIG. 1. Perigynia of *Carex*; adaxial view (left), transverse section (bottom right), and achene adaxial view (top right). a. *C. athrostachya* (*Moran & Thorne 14491*, SD). b. *C. brevior* (*Bartlett 10088*, MICH). c. *C. curviculmis* (*Rzedowski 21567*, TEX). d. *C. festivelloides* (*Pringle 1402*, GH). e. *C. interjecta* (*Freudenstein 2178*, MICH). f. *C. lagunensis* (*González & Rzedowski 1889*, ENCB). g. *C. longii* (*Reznicek 8111 & Reznicek*, MICH). h. *C. microptera* (*Tenorio L. 793 & Romero T.*, MICH). i, j. *C. orizabae* (i. *Vega 432*, NY; j. *Anderson 12947*, MICH). k. *C. peucophila* (*Reznicek 8067 & Reznicek*, MICH). l. *C. subfusca* (*Tallent 744*, MICH). m. *C. tolucensis* (*Mick & Roe 236*, MICH). n. *C. tribuloides* (*Pringle 7802*, GH). o. *C. wootonii* (*[Schneider] 954*, MICH). Scale: bar = 1 mm. Drawn by Susan A. Reznicek.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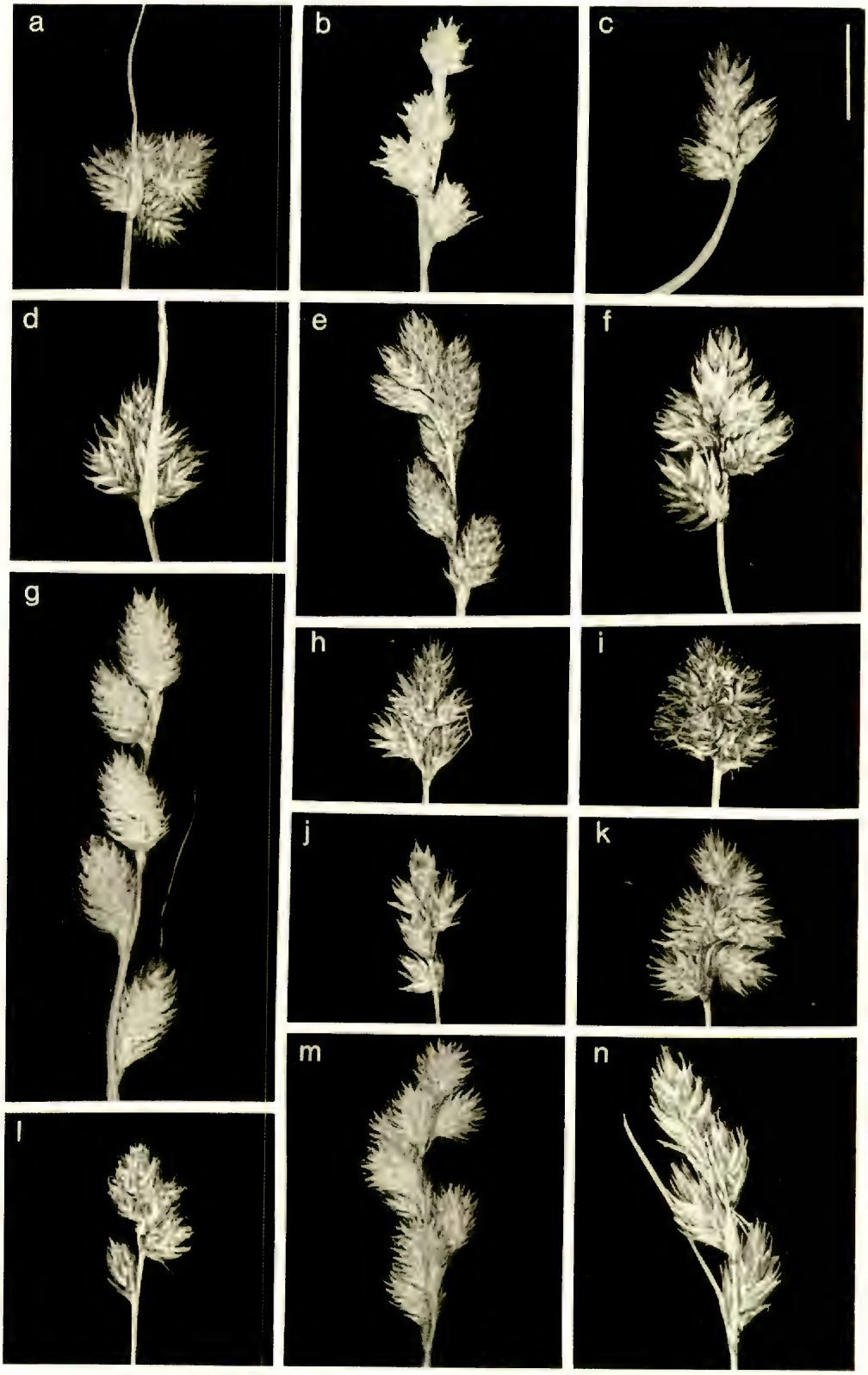
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Hermann (1970) noted that this species and *C. subfusca*, also occurring in the Sierra San Pedro Mártir, can be difficult to distinguish if the prolonged bracts of *C. athrostachya* are lacking (or if an inflorescence of *C. subfusca* is found with unusually elongate bracts). He noted several very subtle characters that tell these two species apart, but normally the perigynia of *C. athrostachya* tend to be longer (3–4.6 mm) than at least Baja populations of *C. subfusca* (2.7–4.1 mm) and proportionately narrower, 2.5–3.2 (–4.5) times as long as wide in *C. athrostachya* versus 1.9–2.6 times as long as wide in *C. subfusca*. If an individual of *C. athrostachya* were found that lacked the elongated lower inflorescence bracts, it would key here to *C. microptera*, from which it could be distinguished by its usually narrower and much more narrowly winged perigynia only 1–1.5 mm wide. *Carex microptera* has perigynia 1.2–1.9 (–2.4) mm wide, which are broadly thin-winged. In addition, the perigynia of *C. athrostachya* are more gradually tapered to an indistinct beak. The perigynium beaks of *C. microptera* are well defined. The inflorescences of *C. athrostachya* are mostly substantially paler, with yellowish brown to reddish brown scales. *Carex microptera* has darker reddish brown to purplish brown pistillate scales, and the inflorescences are thus darker overall.

Carex athrostachya was first reported from Mexico in Hermann (1974), based on *Balls 4202*. González E. (1990) reported two additional collections, *González E. 1151* and *1142*. These collections, all from high elevations in the Transvolcanic Belt, are here referred to *C. orizabae*.

2. Carex brevior (Dewey) Mackenzie in Lunell, Amer. Midl. Naturalist 4: 235. 1915. *Carex straminea* var. *brevior* Dewey, Amer. J. Sci. 11: 158. 1826.—TYPE: U.S.A. [Massachusetts: western Massachusetts,] *Dewey s.n.* (holotype: ?GH, not located). Figs. 1b, 2b.

Cespitose in small clumps from thick, woody, very short-creeping rhizomes; fertile culms 15–120 cm tall, ± stiffly erect, trigonous, smooth except just below inflorescence, where usually finely scabrous-angled; bladeless basal sheaths pale brown, disintegrating into short, dark brown fibers. Leaves 3–5, on the lower 1/5–1/3 of the culm; blades 2.5–30 cm long, 1.5–3.5 mm wide, plicate, glabrous or ± papillose adaxially, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 1.5–8 cm long, tightly enveloping culms, glabrous, green, sometimes white-mottled; the inner band of sheaths glabrous, whitish hyaline, prolonged up to 2 mm beyond the leaf bases, the apex concave, whitish hyaline to pale brown; ligules 0.7–2.3 mm long, rounded, the free portion entire, up to 0.4 mm long. Vegetative culms different from the fertile, fully developed only after the perigynia are largely shed, annual, 3–30 cm tall with ca. 9–20 leaves; leaves tristichous and mostly clustered in the upper 1/3 of the culm, often slightly larger than those of the fertile culms. Inflorescences (1.3–) 2.5–6.5 cm long, erect to arching, the upper spikes usually overlapping, the lowest two spikes (3–) 6–14 (–23) mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous,

FIG. 2. Inflorescences of *Carex*. a. *C. athrostachya* (*Moran & Thorne 14491*, SD). b. *C. brevior* (*Bartlett 10088*, MICH). c. *C. curviculmis* (*Rzedowski 21567*, TEX). d. *C. festivelloides* (*Pringle 1402*, GH). e. *C. interjecta* (*Freudenstein 2178*, MICH). f. *C. lagunensis* (*Vega 426*, MEXU). g. *C. longii* (*Arsène 9909*, US). h. *C. microptera* (*Spellenberg 11031 & Bacon*, MICH). i. *C. orizabae* (*Rzedowski 36660c*, ENCB). j. *C. peucophila* (*Rzedowski 22999*, ENCB). k. *C. subfusca* (*Moran 30986*, SD). l. *C. tolucensis* (*Mick & Roe 236*, MICH). m. *C. tribuloides* (*Pringle 7802*, GH). n. *C. wootonii* (Arizona, Coconino Co., *Tallent 401*, MICH). Scale: bar = 1 cm.

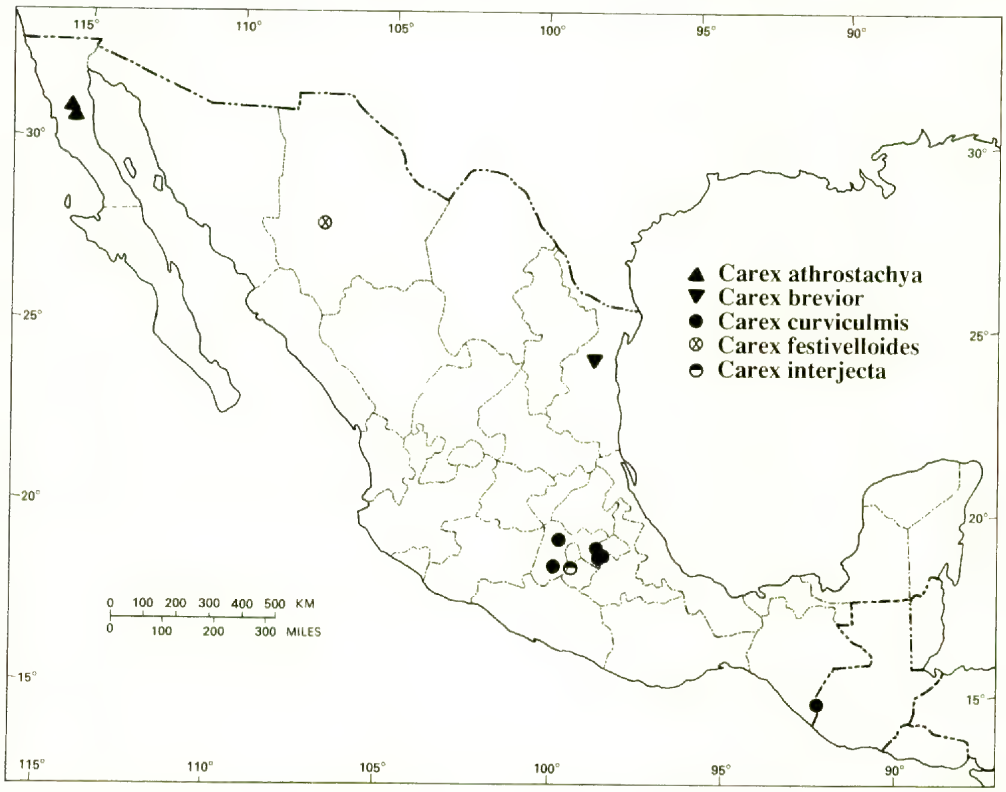

FIG. 3. Distribution of *Carex athrostachya*, *C. brevior*, *C. curviculmis*, *C. festivelloides*, and *C. interjecta*.

0.5–1.5 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes (2–) 3–6, gynaecandrous; terminal spikes often slightly larger than the lateral and with a longer staminate base, but otherwise essentially similar, clavate-ovoid, 8–16 (–24) mm long, pistillate portion 5–10 mm long, 4.5–8 mm wide, (10–) 25–45-flowered, staminate portion 3–9 (–14) mm long, 1.5–2 mm wide, ca. 3–12-flowered. Pistillate scales 2.6–4.3 mm long, 1.2–1.8 mm wide, narrowly ovate, acute, pale yellowish brown to pale reddish brown with a narrow green center and narrow hyaline margins, 1-nerved. Staminate scales 3.1–5.2 mm long, 1.1–1.8 mm wide, narrowly ovate, acute to acuminate, pale yellowish brown to pale reddish brown with a narrow green center and narrow hyaline margins, 1-nerved. Perigynia (2.9–) 3.4–4.6 mm long, (2.1–) 2.4–3.2 (–3.4) mm wide, 1.1–1.7 times as long as wide, ascending, plano-convex with ± orbicular bodies 2.1–3.5 mm long, 0.7–1.3 times as long as wide and 2.1–3.5 times as long as the beak, widest 1.2–1.6 mm above base, broadly thin-winged and finely serrulate-margined except near base, contracted into a beak, pale yellowish brown to brown, glabrous, sessile, adaxial side nerveless or rarely very faintly 1–5-nerved over achene, abaxial side 3–9-nerved over achene; beaks 0.8–1.5 mm long, strongly flattened and serrulate-margined to apex, the apex bidentate with scabrous-margined teeth 0.1–0.5 mm long. Achenes 1.5–2 mm long, 1.2–1.6 mm wide, 1.1–1.4 times as long as wide, biconvex, broadly ovate-oblong to ± orbicular, pale brown, short-stipitate; style straight; stigmas 2. Anthers 3, 1.5–2.4 mm long. Chromosome number: $n = 34$ (Löve & Löve 1981).

A species of dry to moist sites in prairies and plains, collected only once in Tamaulipas (Fig. 3) in an unspecified habitat at ca. 1000 m.

Specimen Examined. Tamaulipas: La Vegona, vicinity of San José, Sierra de San Carlos, 5 Jul 1930, *Bartlett 10088* (MICH).

Carex brevior is widely distributed throughout North America from British Columbia to Quebec and south, in the west to Arizona and Texas. The single Mexican occurrence is disjunct from the nearest localities in central Texas. *Carex brevior* is unique among Mexican species of section *Ovales* in having ± orbicular perigynium bodies essentially nerveless over the achene adaxially. *Carex longii* may sometimes have nearly orbicular perigynium bodies, although they are usually more obovate, but it differs from *C. brevior* in several features. *Carex longii* has elongate vegetative culms ca. 30–100 cm tall, herbaceous, green inner bands on at least the upper sheaths, perigynia distinctly 3–9-nerved over the achene adaxially and widest 1.4–2 mm above base, and achenes 0.8–1.1 mm wide and 1.5–1.7 times as long as wide. *Carex brevior* has shorter vegetative culms 3–30 cm tall, whitish hyaline inner bands to the sheaths, perigynia nerveless or rarely very faintly 1–5-nerved over achene adaxially and widest 1.2–1.6 mm above base, and achenes 1.2–1.6 mm wide and 1.1–1.4 times as long as wide. An additional, subtle difference is that in *C. brevior*, the perigynium body is abruptly contracted to a relatively narrow beak, whereas in *C. longii* the body tapers more gradually to a wide beak. Nevertheless, incomplete or immature specimens can be difficult to determine with certainty.

A somewhat similar species, *Carex brittoniana* L. H. Bailey, is frequent locally in Texas, where it occurs along the Rio Grande even as far south as the vicinity of Brownsville. It seems almost certain that it occurs also in northernmost Tamaulipas. The perigynia have ± orbicular bodies similar in shape to *C. brevior*, but are much larger, (5.5–) 6–8.3 mm long and 3.7–6 mm wide, and have longer beaks 1.5–3.4 mm long. The key in Jones and Reznicek (1991) provides further distinctions.

3. Carex curviculmis Reznicek, sp. nov.—Type: Mexico. México: Vertiente SW del Ixtaccíhuatl, La Joya, Cañada de Alcalican, 1 Nov 1965, *Rzedowski 21567* (holotype: MEXU!; isotypes: DS! ENCB! LL! MICH! TEX! US! VDB! WIS!). Figs. 1c, 2c.

Plantae laxe cespitosae vel ± coloniales; culmi fertiles 7–55 cm alti; vaginae basales pallide brunneae, glabrae. Folia 3–8; laminae 3–18 cm longae, 1–3 mm latae; vaginae ca. 1–6 mm longae, ventraliter albido-hyalinae, glabrae; ligulae 1–3.2 mm longae. Inflorescentiae 0.9–2 cm longae; spicae gynaecandrae, ovoideae, 4.8–12 mm longae, bracteae infimae glumaceae vel setaceae, 0.4–0.8 (–1.6) cm longae. Perigynia (4–) 4.3–5.4 mm longa, 1.4–1.8 mm lata, 2.6–3.3plo longiora quam latiora, ascendentia, planoconvexa, corporibus ellipticis, 2.8–4 mm longis, 1.8–2.3plo longioribus quam latioribus, in rostrum serrulatum 1.3–1.5 (–1.7) mm longum attenuata. Achenium 1.7–2 mm longum, (1.1–) 1.2–1.4 mm latum, planoconvexum. Styli marcescentes; stigmata 2. Antherae 3, 1.4–2.7 mm longae.

Loosely cespitose or ± colonial in small patches by short-creeping rhizomes, rhizomes up to 7 mm long between shoots; fertile culms 7–55 cm tall, stiff but arcuate to ± nodding, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, ± persistent. Leaves 3–8, on the lower 1/10–1/3 of the culm; blades 3–18 cm long, 1–3 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 1–6 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths

glabrous, whitish hyaline, sometimes prolonged up to 1 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 1–3.2 mm long, rounded, the free portion entire, up to 0.3 mm long. Vegetative culms ca. 1–6 cm tall with 5–10 leaves; leaves tristichous and mostly clustered in the upper 1/2 of the culm. Inflorescences 0.9–2 cm long, capitate-ovoid, the upper spikes overlapping, the lowest two spikes 1.5–6 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or occasionally setaceous, 0.4–0.8 (–1.6) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 3–5 (–6), gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 4.8–12 mm long, pistillate portion 4–9.5 mm long, 3.5–5 mm wide, ca. 5–20-flowered, staminate portion 0.8–2.5 mm long, appressed against pistillate portion, ca. 1–4-flowered. Pistillate scales 3.2–4.3 mm long, 1.6–2.3 mm wide, ovate, acute, reddish brown with a narrow green center and narrow hyaline margins, 1–3-nerved. Staminate scales ca. 3.5–4.6 mm long, ca. 1.4–2.2 mm wide, narrowly ovate, acute to acuminate, reddish brown with a narrow green center and hyaline margins, 1–3-nerved. Perigynia (4–) 4.3–5.4 mm long, 1.4–1.8 mm wide, 2.6–3.3 times as long as wide, ascending, plano-convex with elliptic bodies 2.8–4 mm long, 1.8–2.3 times as long as wide and 1.7–2.9 times as long as the beak, widest 1.4–1.9 mm above base, narrowly and thickly winged and serrulate-margined above the widest point, the wings ± arched forward, gradually tapered into a beak, green to pale brown, glabrous, sessile, adaxial side nerveless or faintly 1–5-nerved over achene, abaxial side faintly (0–) 1–9-nerved over achene; beaks 1.3–1.5 (–1.7) mm long, strongly flattened and serrulate-margined but with the apical 0.3–0.6 mm terete and smooth, the apex obliquely bidentate with scabrous-margined teeth up to 0.4 mm long. Achenes 1.7–2 mm long, (1.1–) 1.2–1.4 mm wide, 1.2–1.6 times as long as wide, biconvex, ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 1.4–1.8 (–2.7) mm long. Chromosome number unknown.

An uncommon species of moist alpine meadows, streambanks, and open moist conifer forests at 3000–4000 (–4600?) m in the Transvolcanic Belt, with one station known in Chiapas (Fig. 3). This is a species of the upper slopes of the high volcanos, occurring on Volcán Ixtaccíhuatl, Volcán Tacaná, and the Nevado de Toluca, with one station at Palomas in the State of México. Fruiting specimens have been collected from July through February.

Additional Specimens Examined. Chiapas: Mpio. Unión Juárez, SE side of the summit of Volcán Tacaná, 10 Nov 1972, *Breedlove 29327* (CAS, MICH, TEX).—México: Mpio. Ixtapaluca, N slope of Volcán Ixtaccíhuatl, main road from hwy to Estación Experimental Zoquiapan, 8 km S of Río Frío, 8 Oct 1983, *Anderson 12948* (MICH); Iztaccíhuatl, NW side of mtn, ca. 9 km E of San Rafael, 16 Jul 1959, *Beaman 2849* (MSC); SW slopes of Volcán Ixtaccíhuatl ca. 8 km N of Paso de Cortés, 26 Feb 1988, *Reznicek 8118 & Reznicek* (MICH); W slopes of Nevado de Toluca, 35 km (road) SW of Toluca on hwy 130, 29 Aug 1965, *Roe et al. 1475* (ENCB, US, WIS); Mpio. Chalco, Llano Grande, km 54 carretera México-Puebla, 26 Jul 1964, *Rzedowski 18465* (MICH, MSC; mixed with *C. orizabae*); Mpio. Iturbide, Palomas, 8 Aug 1968, *Rzedowski 25929* (DS, MICH, both mixed with *C. peucophila*; MSC, ENCB); Mpio. Amecameca, La Joya de Alcalican, extremo SSW del Ixtaccíhuatl, 13 Nov 1977, *Rzedowski 35545* (VDB), 2 May 1980, *Rzedowski 36654a* (ENCB); La Cienega, región de Peñas Cuatas, cerca de la Cabeza del Iztaccíhuatl, 14 Jan 1981, *Rzedowski 37192* (ENCB); 55 km SE of Mexico City, 13 Jul 1942, *Weaver 779* (NY).—Puebla: S slope of Volcán Ixtaccíhuatl, 23 Oct 1966, *Hermann 20849* (MICH, US).

Endemic to Mexico, as far as known, *Carex curviculmis* resembles *C. peucophila* rather closely, and has been included with it by all past authors. There is, however, an apparently real discontinuity in morphology between the two; the

longer, narrow perigynia (4–) 4.3–5.4 mm long and 2.6–3.3 times as long as wide, and longer beaks 1.3–1.5 (–1.7) mm long set off *C. curviculmis* relatively clearly. In *C. peucophila*, the perigynia are (3.3–) 3.5–4.4 (–4.7) mm long and 1.8–2.4 (–2.6) times as long as wide with a shorter beak 0.6–1.2 (–1.5) mm long. The two species are similar in habit with short-creeping rhizomes and arching or curved fertile culms, and immature or depauperate specimens can be difficult or impossible to determine. The culms of *C. curviculmis* are generally stiffer and thicker, but there is overlap in this feature. The epithet *curviculmis* alludes to the arching or curved culms typical of this species.

Whereas *C. peucophila* has an extremely wide altitudinal range from (2000–) 2400–3800 (–3950) m, *C. curviculmis* is apparently confined to elevations above 3000 m. One collection, *Hermann 20849*, gives an elevation of 15000 ft (4600 m), but this seems too high, as it would place the species virtually at the snowline on the barren volcanic ash fields. A single mixed collection has been seen, indicating that the two can grow together in the same habitat. *Rzedowski 36654a*, tentatively placed here, is too immature to be determined with absolute certainty.

4. Carex festivelloides Reznicek, sp. nov.—Type: MEXICO. Chihuahua: Sierra Madre, 3 Oct 1887, *Pringle 1402* (holotype: MEXU!; isotypes: F! GH! MICH! NY-2 sheets! RSA! US! WIS!). Figs. 1d, 2d.

Plantae dense cespitosae; culmi fertiles 15–50 cm alti; vaginae basales pallide brunneae, glabrae. Folia 3–5; laminae 3–20 cm longae, 1.3–3.2 mm latae; vaginae ca. 2.5–7 mm longae, ventraliter albido-hyalinae, glabrae; ligulae 1.3–3.2 mm longae. Inflorescentiae 1–2.3 cm longae; spicae gynaecandrae, ovoideae, 4.5–11.5 mm longae, bracteae infimae laminis 1.2–6 (–8) cm longis, ca. 2 mm latis, evaginatis. Perigynia (3.8–) 4.3–5.8 mm longa, (1.3–) 1.5–1.9 mm lata, 2.7–3plo longiora quam latiora, ascendentia, planoconvexa, corporibus ellipticis, 2.8–3.8 mm longis, 1.9–2.2plo longioribus quam latioribus, in rostrum serrulatum 1.3–1.6 mm longum contracta. Achenium 1.7–2 mm longum, 1–1.3 mm latum, planoconvexum. Styli marcescentes; stigmata 2. Antherae 3, 1.6–2.8 mm longae.

Cespitose in dense clumps; fertile culms 15–50 cm tall, erect, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, ± persistent. Leaves 3–5, on the lower 1/6–1/3 of the culm; blades 3–20 cm long, 1.3–3.2 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2.5–7 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, sometimes prolonged up to 1 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 1.3–3.2 mm long, rounded, the free portion entire, up to 0.4 mm long. Vegetative culms, ca. 3–6 cm tall with 4–9 leaves; leaves tristichous and mostly clustered in the upper 1/2 of the culm. Inflorescences 1–2.3 cm long, ± capitate-ovoid, but with the spikes usually distinct but strongly overlapping, the lowest two spikes ca. 1–5 mm distant, spikes single at nodes, sessile, lowermost bracts setaceous to ± leafy, 1.2–6 (–8) cm long and up to ca. 2 mm wide, conspicuous, sheathless but dilated at base, the upper bracts much reduced; spikes (2–) 3–6 (–8), gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 4.5–11.5 mm long, pistillate portion 5–11 mm long, 4–8.5 mm wide, (4–) 7–20-flowered, staminate portion 0.5–1 mm long, appressed against the pistillate portion, 1–3-flowered. Pistillate scales 3.2–4.5 mm long, 1.4–2.1 mm wide, ovate, acute, reddish brown with a narrow green center

and hyaline margins, 1-nerved. Staminate scales ca. 2.9–3.6 mm long, 1.5–2.3 mm wide, ovate, acute, reddish brown with a narrow green center and hyaline margins, 1-nerved. Perigynia (3.8–) 4.3–5.8 mm long, (1.3–) 1.5–1.9 mm wide, 2.7–3 times as long as wide, ascending, plano-convex and strongly flattened with elliptic bodies 2.8–3.8 mm long, 1.9–2.2 times as long as wide, and 2.1–2.4 times as long as the beak, widest 1.3–1.9 mm above base, broadly thin-winged and serrulate-margined except near base, tapered into a beak, green to pale brown, glabrous, sessile, adaxial side nerveless or nearly so over achene, abaxial side faintly (0–) 3–7-nerved over achene; beaks 1.3–1.6 mm long, strongly flattened and serrulate-margined to apex, the apex bidentate with scabrous-margined teeth up to 0.5 mm long. Achenes 1.7–2 mm long, 1–1.3 mm wide, 1.5–1.8 times as long as wide, biconvex, ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 1.6–2.8 mm long. Chromosome number unknown.

Known only from the type, collected in "Moist soil," presumably in an alpine meadow, at 2900 m in Chihuahua (Fig. 3). Fruit was mature in early October. Pringle does not give a specific locality on the label, but from September 10 to October 11, 1887, he was encamped a few miles south of Ciudad Guerrero, in central Chihuahua. The type was gathered from "the summit five or six miles from camp, and 9500 feet above sea level by my aneroid" (Davis 1936).

Pringle 1402 is a paratype of *C. egglestonii* var. *festivelliformis* F. J. Herm., but Hermann's (1960) concept of his variety was confounded by the fact that it was based on two different species; the type belongs with *C. wootonii*. *Pringle 1402*, much more than the type, does superficially resemble plants called *C. festivella* from the Rocky Mountains (hence the epithet *festivelloides*) and was so annotated and reported by Mackenzie (1931). *Carex festivella* was considered merely a robust southern form of *C. microptera* by Whitkus and Packer (1984), but in any event, several characters separate *C. festivelloides* clearly. *Carex festivelloides* apparently has consistently elongated lower inflorescence bracts, perigynium beaks flattened and serrulate-margined virtually to the prominently bidentate apex, and achenes 1–1.3 mm wide. The "*C. festivella*" form of *C. microptera* lacks consistently elongated lower inflorescence bracts, has perigynium beaks terete and smooth apically, and has achenes only ca. 0.8–1 mm wide. *Carex festivelloides* differs dramatically from *C. egglestonii* Mack. in having much smaller and narrower perigynia.

Because of the elongated lower inflorescence bracts, *C. festivelloides* might be thought to be close to *C. athrostachya*, but the bract character appears to be a convergence. *Carex athrostachya* has terete beak apices that are barely bidentulate, narrower, smaller perigynia and achenes (see key), and shorter anthers, among other differences. If individuals of *C. festivelloides* that lack elongated lower inflorescence bracts were found, they would key here to *C. curviculmis*, from which they could be separated by their densely cespitose habit, erect fertile culms, broadly thin-winged perigynia, and usually longer anthers 1.6–2.8 mm long. *Carex curviculmis* has a loosely cespitose habit, with the rhizomes short-creeping, arcuate to ± nodding fertile culms, narrowly thick-winged perigynia, and usually shorter anthers 1.4–1.8 (–2.7) mm long.

5. Carex interjecta Reznicek, sp. nov.—TYPE: MEXICO. Morelos: near lagoons in Lagunas de Zempoala National Park, 29 Jul 1987, *Freudenstein 2178* (holotype: MICH!). Figs. 1e, 2e.

Plantae dense cespitosae; culmi fertiles 40–60 cm alti; vaginae basales pallide brunneae, glabrae. Folia ca. 4–5; laminae ca. 5–20 cm longae, ca. 1.8–3.2 mm latae; vaginae ca. 2–6 mm longae, ventraliter albido-hyalinae, glabrae; ligulae 2.5–5.5 mm longae. Inflorescentiae 2.5–3.5 cm longae; spicae gynaecandrae, ovoideae, 6–11 mm longae, bracteae infimae glumaceae vel setaceae, 0.8–3 cm longae. Perigynia (3.5–) 3.7–4.5 mm longa, 1.3–1.8 mm lata, 2.2–2.6plo longiora quam latiora, adpressa, ± biconvexa, corporibus ellipticis vel aliquantum obovoideis, 2.4–3 mm longis, 1.5–1.8plo longioribus quam latioribus, in rostrum serrulatum 1.1–1.5 mm longum contracta. Achenium ca. 1.4–1.7 mm longum, ca. 0.9–1.1 mm latum, biconvexum. Styli marcescentes; stigmata 2. Antherae 3, ca. 1.2–1.5 mm longae.

Cespitose in small clumps; fertile culms 40–60 cm tall, erect, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, rapidly disintegrating. Leaves ca. 4–5, on the lower 2/5–2/3 of the culm; blades ca. 5–20 cm long, ca. 1.8–3.2 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2–6 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, sometimes prolonged up to 1.5 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 2.5–5.5 mm long, rounded, the free portion entire, up to 0.4 mm long. Vegetative culms unknown. Inflorescences 2.5–3.5 cm long, elongate, the upper spikes overlapping, the lowest two spikes 3–9 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.8–3 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 6–9, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 6–11 mm long, pistillate portion 5–9 mm long, 3.5–5 mm wide, ca. 12–50-flowered, staminate portion 1–2.5 mm long, ca. 1.5 mm wide, ca. 1–3-flowered. Pistillate scales 2.8–3.8 mm long, 1.4–1.7 mm wide, ovate, obtuse to acute, reddish brown with a narrow green center and narrow hyaline margins distally, 1-nerved. Staminate scales 2.4–3.1 mm long, ca. 1.4–2.1 mm wide, ovate, acute, reddish brown with a narrow green center and hyaline margins, 1–3-nerved. Perigynia (3.5–) 3.7–4.5 mm long, 1.3–1.8 mm wide, 2.2–2.6 times as long as wide, appressed, ± biconvex with elliptic to somewhat obovate bodies 2.4–3 mm long, 1.5–1.8 times as long as wide, and 1.8–2.6 times as long as the beak, widest ca. 1.5–1.7 mm above base, broadly winged and serrulate-margined above the widest point, the wings somewhat arched forward, tapered into a beak, green to pale brown, glabrous, sessile, adaxial side faintly 1–5-nerved over achene, abaxial side faintly 3–9-nerved over achene; beaks 1.1–1.5 mm long, strongly flattened and serrulate-margined but with the apical 0.2–0.4 mm ± terete and smooth, the apex oblique. Achenes ca. 1.4–1.7 mm long, ca. 0.9–1.1 mm wide, ca. 1.5–1.7 times as long as wide, biconvex, narrowly ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, ca. 1.2–1.5 mm long. Chromosome number unknown.

Known only from the type, collected in a moist meadow in Morelos at approximately 2900 m (no elevation given with the specimen) (Fig. 3). Only a few culms on the holotype were fully mature at the end of July, so peak fruiting probably would have been in August.

Carex interjecta is an enigmatic plant that is quite different from other Mexican (and United States) members of section *Ovales*. In aspect, its inflorescences look quite like those of *C. longii*: ± elongate, with ascending, ovoid spikes of appressed perigynia. It also has leafy culms like those of *C. longii* (and *C. tribu-*

loides) with the leaves occurring to 2/5–2/3 of the way up the culm. However, these features are juxtaposed with characteristics typical of most or all the other species of the section found in Mexico, including hyaline inner bands to the sheaths, narrow leaves (1.8–3.2 mm wide), and reddish brown pistillate scales. The epithet *interjecta*, "thrust between," alludes to this juxtaposition of features. The affinities of this evidently uncommon plant are uncertain.

6. Carex lagunensis M. E. Jones, Contr. W. Bot. 18: 26. 23 Aug 1933.—TYPE: MEXICO. Baja California Sur: The Laguna, Laguna Mountains, 22 Sep 1930, *Jones 27592* (holotype: POM!). Figs. 1f, 2f.

Carex diehlii M. E. Jones ex F. J. Hermann, Amer. Midl. Naturalist 51: 268. 1954.—TYPE: MEXICO. Chihuahua: Meadow Valley, Sierra Madre Mts, 17 Sep 1903, *Jones s.n.* (holotype: POM!).

Densely cespitose in small clumps; fertile culms 15–80 cm tall, stiffly erect, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, ± persistent. Leaves 4–8, on the lower 1/7–1/3 of the culm; blades 4–27 cm long, 1.5–4.8 mm wide, plicate, glabrous, coriaceous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2–10 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, sometimes prolonged up to 1.5 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 1.2–3.5 mm long, rounded, the free portion ± entire, up to 0.4 mm long. Vegetative culms poorly known, ca. 2–8 cm tall with ca. 7–10 leaves; leaves tristichous and mostly clustered in the upper 1/2 of the culm. Inflorescences 1.2–2.5 (–3.5) cm long, stiffly erect in a dense to ± loose head, the upper spikes overlapping, the lowest two spikes 1.5–9 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or setaceous, rarely the lowermost leafy, 0.5–1.5 (–6) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes (3–) 4–8 (–10), gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 7–12 mm long, pistillate portion 4–11 mm long, 5–8 mm wide, 8–35-flowered, staminate portion 1–2.5 mm long, appressed against the base of the pistillate portion, ca. 1–4-flowered. Pistillate scales 3.5–4.6 mm long, 1.5–2.5 mm wide, ovate, acute, yellowish brown to reddish brown with a narrow green center and narrow hyaline margins, 1 (–3)-nerved. Staminate scales 3.3–4.8 mm long, 1.5–2.5 mm wide, ovate, acute to acuminate, yellowish brown to reddish brown with a narrow green center and hyaline margins, 1 (–3)-nerved. Perigynia (3.5–) 4.3–5.4 mm long, (1.6–) 2–2.6 (–2.8) mm wide, 1.7–2.2 (–2.6) times as long as wide, ascending, plano-convex with elliptic to ± suborbicular bodies 2.7–4.1 mm long, 1.2–2 times as long as wide and (2.2–) 2.5–4 times as long as the beak, widest 1.3–2.1 mm above base, thickly and narrowly winged and serrulate-margined above the widest point, the wings arched forward, tapered into a beak, green to pale brown, glabrous, coriaceous, sessile, adaxial side nerveless or up to faintly 7-nerved over achene, abaxial side ± faintly 3–9-nerved over achene; beaks 0.8–1.2 (–1.5) mm long, strongly flattened and serrulate-margined to apex, the apex irregularly bidentulate with scabrous-margined teeth up to 0.3 mm long. Achenes 1.6–2.4 mm long, 1.2–1.7 mm wide, 1.2–1.6 times as long as wide, biconvex, broadly ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, (1.6–) 1.8–2.8 mm long. Chromosome number unknown.

A species of wet meadows, streambanks, marsh edges, and seepy slopes in pine-oak forest at 1900–3100 m occurring from southern Baja and Chihuahua

south along the Sierra Madre Occidental to the Distrito Federal and the State of México (Fig. 4). Fruiting occurs from July through November.

Additional Specimens Examined. Baja California Sur: Sierra de la Laguna, 24 Jan [1890], *Brandegee s.n.* (UC); 19 Oct 1893, *Brandegee s.n.* (UC); S of Pico La Aguja, Sierra La Laguna, 22 Oct 1977, *Breedlove 43276 & Axelrod* (CAS, MEXU, MO); *Breedlove 43393 & Axelrod* (CAS, MEXU).—Chihuahua: Majalca, 24 Jun 1936, *LeSueur 1103* (F, GH, TEX); Rio Tomochik, along route 14, 10 miles W of town, 9 Jun 1976, *Pinkava 13252* (MSC); Mpio. Bocoyna, ejido de San Ignacio Arareco, 2 Aug 1977, *Weber & Bye 7832* (GH, MEXU, MICH, SD).—Distrito Federal: Lomas de San Angel, Jul 1930, *Lyonnet 723* (CAS, MEXU, US); Delegación de Villa A. Obregón, 3 km al SW de Santa Fé, 6 Oct 1968, *Rzedowski 26329* (CAS); Delegación de Cuajimalpa, Desierto de los Leones, 9 Jul 1944, *Sharp & Gilly 19* (MICH).—Durango: Mpio. Pueblo Nuevo, alredores de Coyotes, 21 Aug 1981, *González E. & Rzedowski 1889* (ENCB); Mpio. El Salto, alrededores del Mil Diez, 2 km al N de El Salto, 27 Jun 1982, *Hernández 7449 & Tenorio* (MEXU); Mpio. El Salto, 4 km al E de El Salto, 1 Jul 1982, *Hernández 7512 & Tenorio* (MEXU, RSA); along Devil's Backbone of Sierra Madre Occidental, 98 road miles NE of Mazatlán on Mex. 40 or 39 road miles SW of El Salto, 23°41'N, 105°42'W, 21 Jul 1969, *Marcks & Marcks 1209* (LL, WIS); about 5 miles N of railroad at Coyotes, 8 Aug 1955, *Maysilles 8283* (MICH); El Salto (Aserraderos), Sierra Madre Occidental, 28 Aug 1934, *Pennell 18369* (MEXU, US); Mpio. El Salto, "El Capulin," 4 km al NE de El Pueblo de 1010, 28 Jun 1982, *Tenorio L. 699 & Romero T.* (MICH, MO); Mpio. El Salto, 1 km al SW de El Salto, 9 Jul 1982, *Tenorio L. 943 & Romero T.* (ENCB, MEXU, MICH, MO); 5 1/2 mi E of El Salto, 12 Aug 1957, *Waterfall 13592 & Wallis* (US).—México: Mpio. Huixquilucan, 2 km al N de Santiago, sobre el camino a Dos Rios, 20 Nov 1979, *González E. 1144* (VDB); Mpio. Ixtapaluca, Estación Experimental de Investigación y Enseñanza de Zoquiapan, 8 km al SW de Río Frío, 28 Aug 1978, *Vega 426* (F, MEXU).—Morelos: near lagoons in Lagunas de Zempoala National Park, 29 Jul 1987, *Freudenstein 2174* (MICH).

Carex lagunensis, as here recognized, is a Mexican endemic characterized by stiffly erect culms and large, wide, coriaceous perigynia (3.5–) 4.3–5.4 mm long, (1.6–) 2–2.6 (–2.8) mm wide, and 1.7–2.2 (–2.6) times as long as wide. Hermann (1974) recognized *Carex diehlii* as a Chihuahuan endemic, but treated *C. lagunensis* as a synonym of *C. peucophila*. Plants from Baja and Chihuahua, however, are quite similar, and distinguishable from *C. peucophila* as noted in the key. In addition, culms of *C. peucophila* are lax and flexuous whereas those of *C. lagunensis* are stiff and erect. *Carex lagunensis* is typically a larger and wider-leaved plant.

Carex lagunensis is perhaps most similar in aspect to *C. multicostata* Mack. of the western United States and may be a close relative of that species. *Carex multicostata* differs in generally having longer perigynium beaks (1.4–2 mm long) and perigynia that are usually finely but distinctly 8–12-nerved over the achene adaxially. *Carex lagunensis* has perigynia with beaks 0.8–1.2 (–1.5) mm long and nerveless or with up to 7 faint nerves over the achene adaxially.

Plants from the Distrito Federal and the State of México occur at higher elevations and are often larger and have darker scales than plants from Chihuahua and Baja, but have very similar perigynia. These plants were often determined as *C. peucophila* or sometimes *C. egglestonii* var. *festivelliformis*, but González E. (1990) noted, under *C. peucophila*, that they were similar to *C. lagunensis*. Durango collections are somewhat intermediate. More collections are needed to assess the significance of this variation. Somewhat immature specimens of *C. lagunensis* can often be recognized by the combination of numerous spikes (usually more than 5), large anthers mostly 1.8–2.8 mm long, cespitose habit, and geographical location. *Pinkava 13252* and *Tenorio L. 999 & Romero T.* are too immature for certain determination.

The two Mexican specimens referred by Hermann (1974) to *Carex xerantica* L. H. Bailey, *Maysilles 8283* and *Waterfall 13592 & Wallis* belong here. *Carex xeran-*

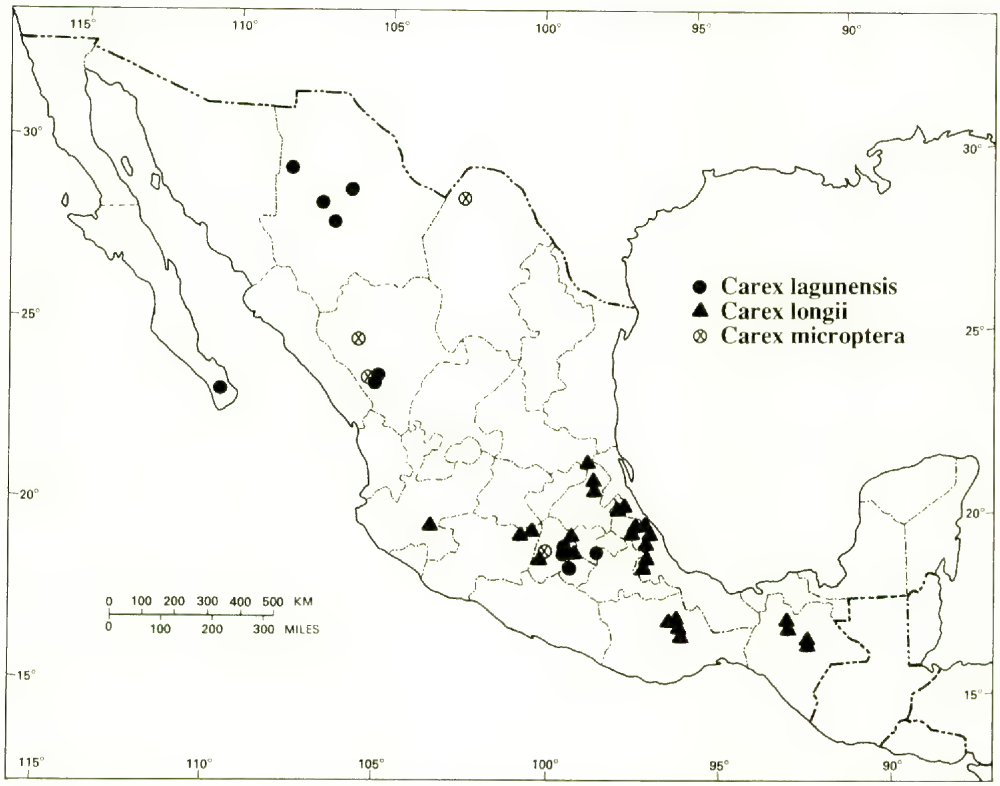

FIG. 4. Distribution of *Carex lagunensis*, *C. longii*, and *C. microptera*.

tica has pistillate scales essentially completely covering the perigynia and a pale inflorescence due to the very wide hyaline margins of the pistillate scales. *Waterfall 13592 & Wallis* clearly has pistillate scales shorter and narrower than the perigynia; *Maysilles 8283* is very immature, so the perigynia are concealed by the scales, but the hyaline margins to the pistillate scales are narrow.

7. Carex longii Mackenzie, Bull. Torrey Bot. Club 49: 373. 1923 [1922].—TYPE: U.S.A. New Jersey: Cape May Co., Cold Spring, 24 Jul 1907, *Long s.n.* (holotype: PH). See Rothrock (1991) for typification. Figs. 1g, 2g.

Carex leporina var. *bracteata* Liebmann, Mex. Halvgr. 76. 1850.—TYPE: MEXICO. Puebla: Huitamalco, 1841, *Liebmann s.n.* (lectotype, here designated: C; isolectotypes: GH! K! P!). Mackenzie (1931) noted "Type from Vera Cruz, Mexico" after his listing of this name in synonymy, but he did not specify which of the two Veracruz specimens Liebmann listed should be the lectotype, nor did he examine any Liebmann material from Veracruz, since apparently only the Puebla sheet is represented in North American herbaria.

Cespitose in small clumps; fertile culms (15–) 30–90 (–140) cm tall, ± erect to often lax and widely spreading, trigonous, smooth; bladeless basal sheaths pale brown, rapidly disintegrating and often absent. Leaves 4–6, on the lower (1/4–) 1/3–3/5 of the culm; blades 5–30 cm long, 1.5–4 (–4.5) mm wide, plicate, glabrous, the margins antrorsely scabrous; leaf sheaths ca. 3–11 cm long, tightly enveloping

culms, glabrous, green and sometimes white-mottled; the inner band of sheaths glabrous or often finely papillose near apex, green with at most a very short, rapidly tapering hyaline zone at the apex (the lower sheaths sometimes with a longer hyaline zone), not or at most slightly prolonged up to 0.5 mm beyond the leaf bases, the apex concave, whitish; ligules 2–6 mm long, rounded, the free portion entire, up to 0.5 mm long. Vegetative culms ca. 30–100 cm tall, annual or sometimes perennating and rooting at the nodes if contacting the soil, leaves ca. 7–15, tristichous and mostly loosely clustered in the upper 1/3 of the culm. Inflorescences (1.4–) 2.2–6 cm long, the upper spikes overlapping, the lowest two spikes 4–14 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.4–7.5 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 2–8, gynaecandrous; terminal spikes often slightly larger than the lateral but otherwise essentially similar, ovoid to clavate-ovoid, 6–17 mm long, pistillate portion 4.5–12 mm long, 4–7.5 mm wide, ca. 10–80-flowered, staminate portion 1–2 (–5.5) mm long, 1–1.5 mm wide, ca. 1–5 (–10)-flowered. Pistillate scales 2.2–3.7 mm long, 1.1–1.8 mm wide, ovate, obtuse to acute, whitish hyaline to pale silvery brown with a green center, 3-nerved. Staminate scales ca. 2.5–5.1 mm long, ca. 1.3–1.8 mm wide, narrowly ovate, acute to acuminate, whitish hyaline to pale silvery brown with a green center, 3-nerved. Perigynia 3–4.6 mm long, 1.6–2.8 mm wide, (1.3–) 1.6–2.2 times as long as wide, appressed, ± biconvex with broadly obovate to ± suborbicular bodies 2.5–3.7 mm long, (1–) 1.2–1.6 times as long as wide, and 2.4–4.1 times as long as the beak, widest ca. 1.4–2 mm above base, broadly winged and serrulate-margined except near base, gradually tapered into a wide beak, green to pale silvery brown, glabrous, sessile, adaxial side 3–9-nerved over achene, abaxial side 5–13-nerved over achene; beaks 0.7–1.3 mm long, strongly flattened and serrulate-margined to apex, the apex obscurely bidentulate with scabrous-margined teeth up to 0.4 mm long. Achenes 1.4–1.7 mm long, 0.8–1.1 mm wide, 1.5–1.7 times as long as wide, biconvex, narrowly ovate-oblong, pale brown, short-stipitate; style straight to slightly sinuous; stigmas 2. Anthers 3, (0.9–) 1.3–2.3 mm long. Chromosome number unknown.

A locally frequent plant, especially in moister areas of Mexico, primarily from southernmost San Luis Potosí to Chiapas along the Sierra Madre Oriental, but with scattered stations elsewhere (Fig. 4.) A species of roadsides, ditches, seepy slopes, streambanks, lakeshores, wet to mesic pastures and meadows, and wet to mesic clearings in forests and forest edges from (500–) 1200–2800 m. One of the weedier species of *Carex* in Mexico, often appearing in recently disturbed ditches and on the shores of reservoirs. Flowering and fruiting occur essentially throughout the year.

Specimens Examined. Chiapas: 2 km N of Jitotol on road to Pichucalco, 20 Oct 1983, *Anderson 13246* (MICH); Mpio. Chamula, 8 miles N of Chamula along road to Chenalho, 19 Jan 1965, *Breedlove 8160 & Raven* (DS, MICH); Mpio. Tenejapa, near crest of ridge in the paraje of Banabil, 10 Oct 1965, *Breedlove 12944 & Raven* (DS, MICH, WIS); Mpio. Jitotol, about 12 km north of Jitotol, 28 Oct 1971, *Breedlove 21479 & Thorne* (DS, NY); Mpio. Tenejapa, Paraje Kurus ch'en, 29 Sep 1972, *Breedlove 28216* (CAS, ENCB, NY); 2 1/2 miles N of Pueblo Nuevo Solist., 22 Jun 1965, *Lathrop 5886* (CAS, RSA, US); Mpio. Tenejapa, at the Paraje Matsab, 12 May 1966, *Ton 940* (DS, F, LL, MICH, MO, RSA).—Distrito Federal: Tlalpan, 9 Dec 1892, *Pringle 5211* (MEXU).—Hidalgo: Mpio. Molango, margin of Lake Atexca below Molango, 9 Nov 1946, *Moore 1942* (GH); 5 km al N de Tlanchinol, sobre la carretera a Huejutla, 21 Sep 1972, *Rzedowski & Madrigal 29413* (ENCB).—Jalisco: Mpio. Gómez Farías, Presa de los Cangrejos, 14 km NE of San Andrés, Dec 1989, *Villa C. et al. 419* (CHAPA, MICH).—México: Presa Tilostoc, 18 Jul 1965, *Lachica et al. FaI-1786* (ENCB); 2 km al W de Cuautitlán, sobre la autopista México-Querétero, 1 May 1973, *Rzedowski 30472*

(ENCB).—MICHOACÁN: Parc San Pedro, vicinity of Morelia, Jul 1909, *Arsène 3031* (GH, ILL, MICH, MO, NY, P, US); Jardin du College, vicinity of Morelia, 27 Jul 1909, *Arsène 3283* (US); Parc San Pedro, vicinity of Morelia, 19 Mar 1909, *Arsène 9909* (US); SE side Morelia along Ave. Ventura Puente, 17 Aug 1966, *Kral 27681* (ENCB, VDB); 14 km al E de Queréndaro, sobre la carretera a Maravatío, 15 Feb 1987, *Rzedowski 42466* (ENCB); Mpio. Morelia, alrededores del balneario Cointzio, ca. de La Mintzita, 9 Jul 1987, *Rzedowski 43571* (ENCB, MICH, XAL).—OAXACA: cerca de Llano de las Flores, 25 km de Ixtlán de Juárez, sobre el camino a Tuxtepec, 23 Oct 1977, *González E. 1020* (ENCB, MEXU); Mpio. Yolox, approx 1 km W of Yolox on the road between Yolox and Quiotepec, 20 Mar 1981, *Martin 444* (MEXU); 34.6 miles NE of Guelatao along hwy 175, 25 Dec 1975, *Reznicek & Gregory M-341* (MICH); Sierra de Juaréz, along hwy 175, 1.5 km by road NE of Cerro Pelón, 21 Feb 1988, *Reznicek 8094 & Reznicek* (MICH); Sierra de Zempoaltepetl, 1.4 km SW of San Pedro y San Pablo Ayutla, 23 Feb 1988, *Reznicek 8111 & Reznicek* (MICH).—PUEBLA: km 184.7 de la carretera México-Tuxpan, 2 Nov 1966, *Cruz C. 1533* (ENCB); near Ocostoc, below Tezuitlan, 18 Aug 1945, *Sharp 45815* (GH, MEXU, NY).—SAN LUIS POTOSÍ: Mpio. Xilitla, 5 km al NE de Ejido de Xilitlilla, 5 May 1959, *Rzedowski 10546* (ENCB, MSC).—VERACRUZ: Orizaba, Sep 1856, *Botteri 187* (P); Ixhuatlancillo, près Orizaba, 4 Jul 1866, *Bourgeau 2588* (GH, K, P); Rancho Guadalupe jardín botánico a 3 km de Xalapa por la carretera vieja a Coatepec, 26 Jul 1976, *Castillo C. et al. 10* (F, XAL); La Calavera, carretera Altotonga-Tlapacoyan, 17 May 1973, *Chazaro & Dorantes 86* (ENCB); Mpio. Coatepec, 4 km Naolinco camino a Coatepec, 12 Aug 1983, *Diego 3615* (ENCB); Mpio. Coatepec, Consolapa, 26 Apr 1983, *Gutiérrez B. & Hernández P. 1325* (XAL); Mpio. Yecuatla, a 3 km NW de Yecuatla, camino Yecuatla-Leona Vicario, 28 Aug 1983, *Gutiérrez B. 1335* (XAL); *Gutiérrez B. 1349* (XAL); Mpio. Yecautla, Santa Rita, carretera Xalapa-Misantla, 26 Apr 1976, *Hernández A. et al. 146* (F, WIS, XAL); ca. 4 km SSW of Xalapa, 10 Oct 1978, *Iltis et al. 953* (WIS); along Río Frío below Teziutlan, Jul 1950, *Johnston 53–669* (TEX); Mpio. Calcahualco, 2 km al NE de Calcahualco, Barranca de Jamapa, 14 May 1985, *Martínez & Espíritu 161* (XAL); Rancho Guadelupe, 3 km W de Jalapa, carretera vieja Jalapa-Coatepec, 23 Aug 1975, *Monroy et al. 57* (ENCB, XAL); 13 km N of Altotonga (19 km by road), on road to Tlapacoyan, vic." Cerro del Aquila," 28 Jun 1980, *Nee & Hansen 18622* (F, MEXU, US, XAL); Jalapa, May 1829, *Schiede & Deppe* (BM, K-2 sheets); Mpio. Altotonga, Xoampolco, 2 Jan 1970, *Ventura A. 305a* (ENCB); Mpio. Atzalan, San Felipe, cerca de la Capilla, 11 May 1970, *Ventura A. 1066* (MEXU).—LOCALITY UNKNOWN: Mexico, 1835, *Müller 1972* (NY).

Carex longii is easily identified because of the combination of herbaceous, green sheaths and wide perigynia 1.6–2.8 mm wide and (1.3–) 1.6–2.2 times as long as wide with ± obovate bodies. The pale color of the inflorescence caused by the green to pale silvery brown perigynia with whitish hyaline to pale silvery brown scales is distinctive once learned. *Carex longii* is widely but rather irregularly distributed in the eastern United States (Rothrock 1991). Its Mexican distribution is somewhat disjunct, with a gap from southern San Luis Potosí to eastern Texas. Elsewhere in the New World, *C. longii* is distributed throughout most of Central America, Bermuda, Cuba, Hispaniola, and northwestern South America south to Ecuador. Farther southeast in South America, from southeastern Brazil to Argentina, occurs the var. *meridionalis* (Kük.) G. A. Wheeler (Wheeler 1987), sometimes recognized as *C. meridionalis* (Kük.) Herter. The description above has been drawn entirely from Mexican material.

In older literature, *Carex longii* is usually united with *C. albolutescens* and reported under the latter name. The typification of *C. longii* and its separation from closely similar plants has been detailed by Rothrock (1991).

8. Carex microptera Mackenzie, Muhlenbergia 5: 56. 1909.—TYPE: U.S.A. Nevada: Elko Co., Deeth, 21 Jul 1908, *Heller 9067* (holotype: NY; isotype: CAS). See Whitkus & Packer (1984) for typification. Figs. 1h, 2h.

Densely cespitose in small clumps; fertile culms 20–90 (–110) cm tall, erect, trigonous, smooth except below inflorescence, where finely scabrous-angled;

bladeless basal sheaths pale brown, ± persistent. Leaves 4–8, on the lower 1/10–1/3 of the culm; blades (4–) 8–25 (–50) cm long, 1.8–3.5 (–5) mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2.5–12 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, occasionally prolonged up to 1 mm beyond the leaf bases, the apex concave, whitish hyaline to pale brown; ligules 1.3–5 mm long, rounded, the free portion entire, up to 0.7 mm long. Vegetative culms 2–9 cm tall with ca. 6–11 leaves; leaves tristichous and mostly clustered in the upper 1/3 of the culm. Inflorescences 0.8–2.6 cm long, broadly ovoid with the spikes difficult to distinguish, the lowest two spikes 1–4 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or occasionally setaceous, 0.5–1.2 (–8) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes (3–) 5–9, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, 5.5–11 mm long, pistillate portion 5–10 mm long, 5–9 mm wide, ca. 15–60-flowered, staminate portion 0.5–2 mm long, appressed against the pistillate portion, ca. 1–5-flowered. Pistillate scales 2.4–4.1 mm long, 0.9–1.7 mm wide, narrowly ovate, acute, reddish brown to purplish brown with a narrow green center and hyaline margins, 1-nerved. Staminate scales 2.1–3.4 mm long, 0.9–1.7 mm wide, lanceolate to narrowly ovate, acute to acuminate, reddish brown to purplish brown with a narrow green center and narrow hyaline margins, 1-nerved. Perigynia (3–) 3.4–4.8 (–5.2) mm long, 1.2–1.9 (–2.4) mm wide, (2.3–) 2.5–3.4 times as long as wide, spreading-ascending, biconvex with elliptic bodies 2.1–3.5 mm long, 1.6–2.4 times as long as wide and 1.5–3 (–3.8) times as long as the beak, widest 0.8–1.8 mm above base, narrowly to broadly thin-winged and serrulate-margined above the widest point, tapered into a beak, green to pale brown, glabrous, sessile, adaxial side nerveless or occasionally faintly 1–5-nerved over achene, abaxial side 5–9-nerved over achene; beaks 1–1.5 (–2.1) mm long, strongly flattened and serrulate-margined but with the apical (0.2–) 0.4–0.7 mm ± terete and smooth, the apex oblique or ± bidentulate with teeth up to 0.3 mm long. Achenes 1.1–1.6 mm long, 0.8–1.1 mm wide, 1.3–1.6 times as long as wide, biconvex, elliptic-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 0.9–2.1 mm long. Chromosome numbers: $n = 40$ (Whitkus & Packer 1984; Whitkus 1991); $n = 41$ (Wahl 1940).

Evidently an uncommon and local species of streambanks, seepy banks, and wet meadows in pine-oak forest at 2100–2650 m, mostly along the Sierra Madre Occidental from Coahuila to the State of México (Fig. 4). Fruiting specimens have been collected from May through August.

Specimens Examined. Coahuila: Mpio. Ocampo, Sierra Madre del Carmen, Cañón Dos, 28°59'N, 102°33'W, 28 May 1975, *Riskind & Patterson 1821c* (LL); Sierra el Carmen, ca. 20 air miles S of U.S. border, ca. 1 km N of Campo Dos in N-S running Cañón el Moreno (= Cn. Dos), 28°59'45"N, 102°36'45"W, 7 Jul 1989, *Spellenberg 9956* (MICH). —Durango: 7.5 mi SW Puerto Buenos Aires along Mex 40, 25 Aug 1965, *Kral 25693* (VDB); Mpio. Santiago Papasquiaro, on the road to Topia and Canelas, 142 km W of the junction with the road from Santiago Papasquiaro to Tepehuanes, 8 km W of El Ojito de Canellones, 19 km E of Cienega de la Nuestra Señora, 28 Jun 1992, *Spellenberg 11031 & Bacon* (MICH); Mpio. El Salto, 4.5 km al SW de El Salto, Brecha El Salto-Pueblo Nuevo, 3 Jul 1982, *Tenorio L. 793 & Romero T.* (MEXU, MICH, MO); 9.3 mi W of El Salto (at river) on Rte. 40, 20 Aug 1979, *Wagner & Solomon 4277* (MO, VDB).—México: Mpio. Villa de Allende, Criadero "San Cayetano," 4 km al N de Agua Escondida, 20 Jun 1982, *Díaz P. 187* (MEXU).

This is the first report from Mexico of this very widespread western North American species distributed from southern Yukon and adjacent Northwest Terri-

tories to Manitoba and South Dakota south to California and New Mexico. *Carex microptera* is a member of the aggregate of species centered on the bipolar disjunct *C. macloviana* (Type: [Falkland Islands], Is. Soledad, *d'Urville 8*, holotype: P!) (Moore & Chater 1971; Whitkus 1988; also Whitkus & Packer 1984, for typification) and is most similar in the Mexican flora to *C. orizabae*, an alpine plant primarily of the Transvolcanic Belt. *Carex microptera* has perigynia green to pale brown even when mature (the tip of the beak, however, sometimes darker), nerveless or only faintly nerved over the achene adaxially, and spreading-ascending in the spikes. The perigynia of *C. orizabae* are normally dark reddish brown to purplish black on the beak and distal portion of the body, ascending-appressed in the spikes, and usually clearly 1–6-nerved over the achene adaxially (the nerves often darker than the rest of the body). *Carex microptera* is densely cespitose, with very little tendency for the rhizomes to become short-creeping, whereas the rhizomes of *C. orizabae* usually are somewhat short-creeping. The aspect of the two species is different; *C. microptera* normally has two-toned inflorescences with the greenish to pale brown perigynia contrasting with the darker scales, and *C. orizabae* usually has very dark inflorescences with the scales and exposed portions of the perigynia the same dark color. Hermann (1971) noted that the perigynia of his *C. volcanica* were "distinctly plano-convex" in contrast to *C. microptera*. The perigynia of *C. orizabae* are generally somewhat less flattened than those of *C. microptera*, but this is a somewhat variable (and difficult to assess) feature.

So far as known, the elevational separation of the two in Mexico is clear; *C. microptera* is mid-montane and occurs from 2100–2650 m, and *C. orizabae* is alpine and occurs from 3000–4300 m. The specimen from the State of México, *Díaz P. 187*, is very immature and its identity is somewhat uncertain, but it is from only 2500 m elevation.

Occasional populations of *Carex microptera* northward in the United States have especially the lowermost perigynia in the spikes more than 2 mm wide, but the few Mexican collections all have narrower perigynia. *Kral 25693* and, to a lesser extent, *Wagner & Solomon 4277*, both from the same area in Durango, are unusual in having some culms with long lower inflorescence bracts and perigynia with a very short, almost evanescent tubular apex to the beak. Accumulation of more collections may demonstrate that these two numbers represent a distinct taxon. In my key, they might be run to *C. athrostachya* (but for the wider perigynia). For differences between *C. athrostachya* and plants here referred to *C. microptera*, see the discussion under *C. athrostachya* .

9. Carex orizabae Liebmann, Mex. Halvgr. 75. 1850.—Type: Mexico. Veracruz: Pico de Orizaba, 14000', in paludis, Sep 1841, *Liebmann s.n.* (holotype: C!; isotypes: GH! K! P!). Figs. 1i, j, 2i.

Carex volcanica F. J. Hermann, Brittonia 23: 144. 1971.—Type: Mexico. México: cerca del Paso de Cortés, entre Popocatépetl e Ixtaccíhuatl, 3550 m, 30 Jan 1966, *Rzedowski 21850* (holotype: US!, isotype: ENCB). [*Carex vulcanica* Elmer, Leafl. Phillip. Bot. 10: 3526. 1938, lacks a Latin description.]

Loosely cespitose in small clumps by very short-creeping rhizomes, rhizomes up to 6 mm long between shoots, fertile culms 15–70 cm tall, erect, trigonous, smooth except just below inflorescence where finely scabrous-angled; bladeless basal sheaths brown, ± persistent. Leaves 3–6, on the lower 1/4–1/2 of the culm;

blades 2–25 cm long, 1.5–4.5 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2–16 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, sometimes prolonged up to 1 mm beyond the leaf bases, the apex shallowly concave, whitish hyaline; ligules 0.8–3.1 mm long, rounded, the free portion entire to ± erose, up to 0.4 mm long. Vegetative culms ca. 2–9 cm tall with 5–10 leaves; leaves tristichous and mostly clustered in the upper 1/5–1/2 of the culm. Inflorescences 1.1–2.2 cm long, densely capitate, the spikes difficult to distinguish, the lowest two spikes 0.5–3 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.3–2.6 (–4) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 4–9 (–12), gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 5–11 mm long, pistillate portion 4.5–10 mm long, 3–6 mm wide, ca. 15–60-flowered, staminate portion 0.5–1 mm long, appressed against the pistillate portion, ca. 1–3-flowered. Pistillate scales 2.8–4.2 mm long, 1.4–2.1 mm wide, narrowly ovate, acute, dark reddish brown to purplish black with a narrow green to brown center and sometimes very narrow hyaline margins, 1-nerved. Staminate scales ca. 2.4–3.6 mm long, ca. 1.2–1.9 mm wide, lanceolate to narrowly ovate, acute, dark reddish brown to purplish black with a narrow green to brown center and sometimes very narrow hyaline margins, 1-nerved. Perigynia 3.2–5.3 mm long, 1.2–1.8 mm wide, (2–) 2.6–3.4 (–4.1) times as long as wide, ascending-appressed, biconvex to ± planoconvex with narrowly ovate to elliptic or rarely ± suborbicular bodies 1.9–3.5 mm long, (1.3–) 1.6–2.7 times as long as wide and (1.1–) 1.5–2.5 (–3.5) times as long as the beak, widest 0.8–2 mm above base, narrowly to broadly thin-winged and serrulate-margined except near base, tapered into a beak, green to pale brown proximally, usually reddish brown to purplish black distally, glabrous, sessile, adaxial side (0–) 1–6-nerved over achene, abaxial side (0–) 1–11-nerved over achene; beaks (0.8–) 1.4–1.9 (–2.1) mm long, strongly flattened and serrulate-margined but with the apical 0.2–0.6 mm ± terete and smooth, the apex obliquely erose to bidentulate with teeth up to 0.2 mm long. Achenes 1.3–1.9 mm long, 0.8–1.1 mm wide, 1.3–1.9 times as long as wide, biconvex, narrowly oblong to ± obovate, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 1.2–2.5 mm long. Chromosome number unknown.

Frequent in wet to mesic alpine meadows and streambanks and open, seepy slopes in pine forest at 3000–4300 m, primarily in the Transvolcanic Belt, with one station in Oaxaca (Fig. 5). Fruiting from July through September, but with the perigynia somewhat persistent.

Additional Specimens Examined. Distrito Federal: alrededores del Llano de la Cieneguilla, arriba del Desierto de los Leones, 5 Sep 1979, *González E. 1109* (ENCB, MEXU, VDB); Delegación de Cuajimalpa, El Pantano, Desierto de los Leones, 20 Nov 1979, *González E. 1142* (ENCB, MEXU); Llano de la Cieneguilla, cerca del Cerro de la Palma, Sierra de las Cruces, 9 Jul 1967, *Rzedowski 23855* (DS, ENCB, LL, MICH, MSC, WIS).—México: Mpio. Ixtapaluca, N slope of Volcán Ixtaccíhuatl, main road from hwy to Estación Experimental Zoquiapan, 8 km S of Río Frío, 8 Oct 1983, *Anderson 12947* (MICH); Paraje Provincial, Mount Popocatépetl, 13 Apr 1938, *Balls 4204* (K-2 sheets, UC, US); Ojos de Agua, Nevado de Toluca, 10 Jul 1938, *Balls 4982* (K, UC, US); between kms 76 and 77 on Amecameca-Popocatépetl road, 2 Aug 1958, *Beaman 2064* (MEXU, MICH, MSC, UC); SW slopes of Volcán Ixtaccíhuatl, along N side of hwy 451 just below (W of) Parque Ixtapopo entrance, 2 km W of road jct. at Paso de Cortés, 16 Jul 1978, *Cochrane & Cochrane 8564* (CAS, ENCB, MICH, MSC, WIS); Mpio. Ixtapaluca, Cañada de Temascatitla, 8 km al S de Río Frío, 17 Sep 1980, *Galván 699A* (ENCB); ladera NW del Popocatépetl, cerca de Paso de Cortés, 2 Dec 1979, *González E. 1151* (ENCB, MEXU, VDB, XAL); Nevado de Toluca, 14 Aug 1964,

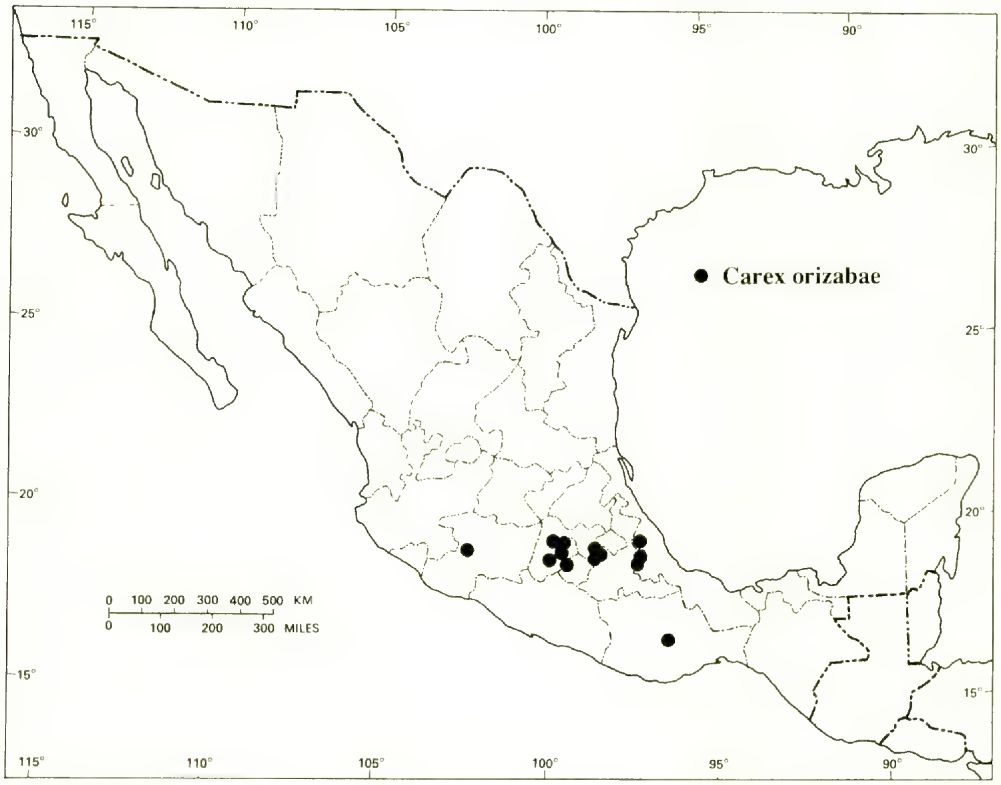

FIG. 5. Distribution of *Carex orizabae*.

González Q. 1238 (ENCB, MICH), *González Q. 1238a* (ENCB); *González Q. 1246* (ENCB); Ixtaccíhuatl, *Purpus 8566* (UC); SW slopes of Volcán Ixtaccíhuatl ca. 8 km N of Paso de Cortés, 26 Feb 1988, *Reznicek 8116 & Reznicek* (MICH), *Reznicek 8117 & Reznicek* (MICH); Mpio. Chalco, Llano Grande, km 54 carretera México-Puebla, 26 Jul 1964, *Rzedowski 18465* (MSC, mixed with *C. curviculmis*); vertiente SW del Ixtaccíhuatl, 4 km al N de la Estación Retransmisora, 15 Jul 1965, *Rzedowski 20157* (DS, ENCB, F, MICH; all mixed with *C. peucophila* except for F sheet); vertiente SW del Ixtaccíhuatl, La Joya, Cañada de Alcalican, 1 Nov 1965, *Rzedowski 21572* (DS, ENCB, MICH); vertiente NW del Ixtaccíhuatl, en el región de Peñas Cuatas, La Cienega, 6 Jan 1966, *Rzedowski 21795* (ENCB, MICH, US); 5 km al W de Paso de Cortés, vertiente NW del Popocatépetl, 9 Oct 1966, *Rzedowski 23269* (ENCB, MICH, MSC); ladera W del Ixtaccíhuatl, arriba de El Salto, Valle de Ayoloco, 19 Nov 1966, *Rzedowski 23477* (ENCB), *Rzedowski 23485* (ENCB); Mpio. Iturbide (Santiago Tlazala), alrededores de la presa Iturbide, 18 Jul 1967, *Rzedowski 25956* (MICH), *Rzedowski 25970* (ENCB); alrededores de la presa Iturbide, 6 km al WNW de Santiago Tlazala, 7 Aug 1977, *Rzedowski 35101* (ENCB, VDB); Mpio. Naucalpan, Villa Alpina, 2 Jul 1978, *Rzedowski 35698* (ENCB); alrededores de la Joya de Alcalican, extremo SW del Ixtaccíhuatl, 26 Nov 1978, *Rzedowski 36014* (ENCB, VDB); Mpio. Amecameca, la Joya de Alcalican, extremo SW del Ixtaccíhuatl, 2 Apr 1980, *Rzedowski 36655a* (VDB), *Rzedowski 36657a* (CAS, MEXU, OS, RSA, VDB), *Rzedowski 36660c* (ENCB); Mpio. Ixtapaluca, Llano Tepochaico, 10 km al S del Llano Grande, 12 Aug 1980, *Rzedowski 36822* (CAS, MEXU, RSA, US, VDB, WIS); Mpio. Ixtapaluca, Cañada de Temascatitla, 12 km al SSW de Río Frío, 14 Sep 1980, *Rzedowski 37014* (ENCB); Ixtaccíhuatl, end of road from Paso de Cortéz and ca. 2 km NE of microwave tower, 22–23 Jun 1974, *Sanders 74092* (LL, MICH); Mpio. Ixtapaluca, Estación Experimental de Investigación y Enseñanza de Zoquiapan, 8 km al SW de Río Frío, 25 Jul 1978, *Vega 358* (ENCB, MEXU, MO), 20 Aug 1978, *Vega 432* (CAS, NY).—Morelos: near lagoons in Lagunas de Zempoala National Park, 29 Jul 1987, *Freudenstein 2177* (MICH).—Michoacán: Mpio. Tancítaro, N slope of Cerro Tancítaro, 22 Jul 1941, *Leavenworth & Hoogstral 1171* (F, ILL).—Puebla: Ixtaccíhuatl, S side of mtn, 1 Aug 1958, *Beaman 1989* (GH, MEXU, MICH, MSC, UC, US, WIS); *Beaman 1992* (GH, MSC, NY, TEX, US, WIS); Estación Forestal San Juan Tetla, 7 Oct 1968, *Boege 921* (GH); laderas orientales del Ixtaccíhuatl, por encima

de San Juan Tlale y San Juan Tetla, 8 Oct 1968, *Ern 314* (ENCB); Campo experimental San Juan Tetla, 17 Aug 1966, *May-Nah 1871* (ENCB); San Juan Tetla, 10 km al SW de San Martín Texmelucan, Llano Zacateotlalpan, 20 Aug 1966, *May-Nah 2142* (ENCB).—OAXACA: Sierra de San Felipe, 25 Aug 1894, *Pringle 5723* (GH).—VERACRUZ: Above los Molinos, Perote, 21 May 1938, *Balls 4560* (K-2 sheets, US); Cofre de Perote, E side of mtn, 6 Aug 1958, *Beaman 2177* (F, GH, MEXU, MSC, TEX, WIS); Cofre de Perote, NW side of mtn, 7 Aug 1958, *Beaman 2202* (MSC, mixed with *C. peucophila*); Mpio. Perote, 11 mi (by air) SE of Perote, 1 km S of Cofre de Perote, 27 Jun 1982, *Diggs et al. 2610* (F, WIS); Pico de Orizaba, 12500', Jun-Oct 1840, *Galeotti 5781* (K, P); Pic d'Orizaba, 1838, *Linden 95* (K, MICH); Mpio. Calcahualco, NE slopes of Pico de Orizaba, 5 km NW of Jacal, 2 km NE of mountaineer shelter "Piedra Grande," 19°04'30"N, 97°15'W, 8 Jul 1982, *Nee & Diggs 24837* (F, NY).

Carex orizabae is a common component of moister alpine grasslands in the Transvolcanic Belt. One collection is known from Oaxaca and one from Guatemala. Normally, the uniformly dark color of the inflorescences provides an easy way to distinguish this species from all other Mexican members of section *Ovales*. Overmature inflorescences, however, tend to fade to a dull straw color, and plants in unusually shaded sites may also be paler, with the perigynia, especially when young, being nearly green. Distinctions from *C. microptera*, the only other similar species of section *Ovales* in Mexico, are given under that species.

Hermann (1971) described this species as *C. volcanica* presumably because he believed, following Mackenzie (1931), that the type of *C. orizabae* belonged with *C. bonplandii*. Neither in his description of *C. volcanica* nor in his Manual (Hermann 1974), however, does he mention the name *C. orizabae* in the synonymy of any species. *Carex orizabae* does not belong with *C. bonplandii*, as it has thin-winged, densely serrulate-margined, and usually ± biconvex to somewhat plano-convex perigynia. *Carex bonplandii* (Type: America meridionalis, *Bonpland*; holotype: P!; isotype: P!) has narrowly thick-winged to nearly wingless perigynia that are only sparsely serrulate-margined and definitely plano-convex.

Carex orizabae is a member of an intricate and very difficult group of section *Ovales* centered on the bipolar *C. macloviana* and recognized by Mackenzie (1931) as his "subsection" *Festivae*. This group, the *C. macloviana* aggregate (Whitkus & Packer 1984), is characterized by having perigynia longer than the usually dark-colored subtending scales, with conspicuous terete and smooth beak apices and usually in small, ovoid spikes in a compact head. *Carex orizabae* can be readily distinguished from *C. macloviana* by its dark reddish brown to purplish black scales; *C. macloviana* has distinctive, copper-colored scales with a metallic luster. As suggested by Hermann (1971), the nearest relative of *C. orizabae* is probably *C. ebenea* Rydb., an alpine species of the southern Rocky Mountains, with which it shares the very dark scales and dark perigynia. *Carex orizabae* can be easily distinguished by its shorter perigynia 3.2–5.3 mm long; *C. ebenea* has perigynia (5.2–) 5.5–7 (–7.8) mm long. Although not noted by Hermann (1971), *C. orizabae* is also similar to the widespread but generally more northern high alpine species *C. haydeniana* Olney, which also has dark scales. *Carex haydeniana* is a compact, short plant never more than about 40 cm tall, and also has generally longer perigynia (4–) 4.5–6.5 mm long, but especially broadly winged, wider perigynia 1.7–2.6 mm wide. The perigynia of *C. orizabae* are only 1.2–1.8 mm wide.

Carex orizabae occasionally, but not consistently, produces some inflorescences with long bracts like those of *C. athrostachya*. Specimens of *C. orizabae* with a few culms having long bracts are, in fact, responsible for reports of *C. athrostachya* from Mexico previous to this treatment. *Carex athrostachya*, known

in Mexico only from Baja, is not a high-alpine plant, has paler scales and perigynia, is densely cespitose, and has the perigynia gradually tapering to an indistinct beak.

Although superficially appearing very uniform because of the compact, uniformly dark heads, *C. orizabae* is actually quite variable, especially in perigynium size and shape. Perigynium bodies range from narrowly ovate to elliptic or nearly orbicular, (1.3–) 1.6–2.7 times as long as wide, with beaks (0.8–) 1.4–1.9 (–2.1) mm long. Amount of development of the wing and the degree of flatness of the perigynium body are also quite variable (see Fig. 1i, j). However, achenes are quite similar in size and shape despite variation in perigynia. Nevertheless, this degree of variation is unusual in a member of the *C. macloviana* aggregate. There appear, however, to be no discontinuities that would define separate taxa nor any discernible geographical or altitudinal patterns to the variation. The species is here circumscribed broadly to include all the variation. A likely hypothesis for the origin of this variation is that *C. orizabae* is actively speciating on the relatively young volcanos of the Transvolcanic Belt, but has not yet differentiated into separate species. It is also possible, however, that *C. orizabae* may already be a complex of sibling species and that detailed field or laboratory studies might uncover subtle ecological or phenological correlations with morphology that would allow its subdivision into segregate taxa.

10. Carex peucophila T. Holm, Contr. U.S. Natl. Herb. 8: 290. 1905. *Carex pinetorum* Liebmann, Mex. Halvgr. 75. 1850, non *Carex pinetorum* Willd. ex Schltdl., 1836. *Carex festiva* f. *humilis* Boeckeler, Linnaea 39: 74. 1881.—TYPE: MEXICO. Veracruz: Pico de Orizaba, in graminosis pinetorum, 12000', Aug 1841, *Liebmann s.n.* (holotype: C!; isotypes: K! P!). Figs. 1k, 2j.

Carex straminea var. *australis* L. H. Bailey, Mem. Torrey Bot. Club 1: 23. 1889.—TYPE: MEXICO. Hidalgo: Real del Monte, *Coulter 1622* (holotype: K!; isotype: K!).

Carex pinetorum var. *elatior* Kükenthal, Das Pflanzenreich. IV, 20, Heft 38: 195. 1909.—TYPE: MEXICO. Oaxaca: Sierra de San Felipe, 8 Jun 1894, *Pringle 4685* (lectotype, designated by Mackenzie, 1931: B, destroyed; isolectotypes: GH! K! LL! MICH! MO! MSC! NY! US!).

Loosely cespitose to ± colonial in small patches by short-creeping rhizomes, rhizomes up to 7 mm long between shoots; fertile culms 6–60 cm tall, lax and flexuous, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, rapidly disintegrating into short, brown fibers. Leaves 4–7, on the lower 1/8–1/4 of the culm; blades 4–25 cm long, 1.2–3 (–4) mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous; leaf sheaths ca. 1.5–6 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, prolonged up to 1.5 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 0.8–3.5 mm long, rounded, the free portion entire to ± erose, up to 0.6 mm long. Vegetative culms 1.5–7 cm tall with ca. 6–9 leaves; leaves tristichous and mostly clustered in the upper 1/4 of the culm. Inflorescences 0.8–2.2 (–2.7) cm long, erect to arching in a short, loose head, the upper spikes overlapping, the lowest two spikes 1–12 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.4–2.4 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 2–5 (–7), gynaecandrous; terminal spikes often slightly larger than the lateral,

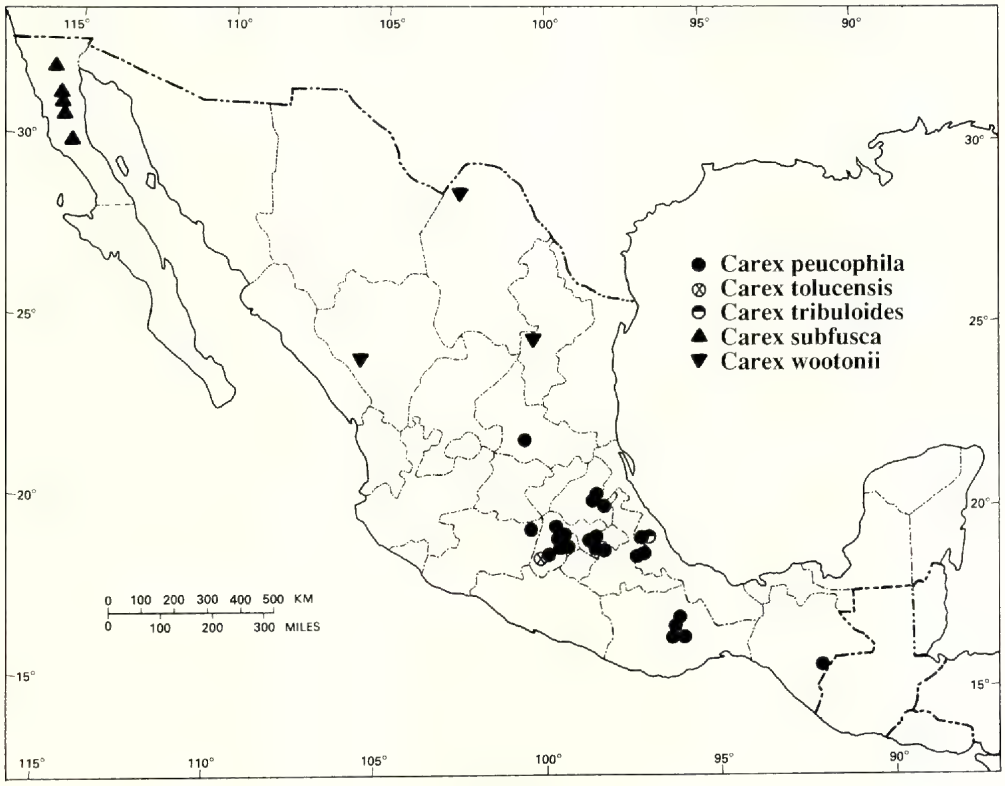

FIG. 6. Distribution of *Carex peucophila, C. subfusca, C. tolucensis, C. tribuloides,* and *C. wootonii.*

but otherwise essentially similar, ovoid, 4.5–11 mm long, pistillate portion 3.5–9 mm long, 3.5–7 mm wide, (2–) 4–25-flowered, staminate portion 1–3 mm long, ca. 1.5 mm wide, ca. 1–4-flowered. Pistillate scales 2.6–4 mm long, 1.6–2.4 mm wide, ovate, acute, yellowish brown to reddish brown with a narrow green center and narrow hyaline margins, 3-nerved. Staminate scales 2.6–4.8 mm long, 1.4–2.3 mm wide, ovate, acute, yellowish brown to reddish brown with a narrow green center and hyaline margins, 1 (–3)-nerved. Perigynia (3.3–) 3.5–4.4 (–4.7) mm long, 1.6–2 (–2.3) mm wide, 1.8–2.4 (–2.6) times as long as wide, appressed-ascending, plano-convex with elliptic-ovate bodies 2.3–3.4 mm long, 1.3–2 times as long as wide and (1.9–) 2.2–4 (–5.4) times as long as the beak, widest 1.1–1.8 mm above base, narrowly and thickly winged and serrulate-margined above the widest point, the wings arched forward, contracted into a beak, green to pale brown or sometimes the body dark reddish brown when ripe, glabrous, sessile, adaxial side nerveless or occasionally faintly 1–4-nerved over achene, abaxial side faintly (0–) 1–5 (–11)-nerved over achene; beaks 0.6–1.2 (–1.5) mm long, strongly flattened and serrulate-margined but often with the apical 0.1–0.3 mm ± terete and smooth, the apex ± bidentulate with scabrous-margined teeth up to 0.4 mm long. Achenes 1.5–1.9 mm long, (1.1–) 1.2–1.5 mm wide, 1.1–1.6 times as long as wide, biconvex, ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 1.2–1.8 mm long. Chromosome number: $n = 37$ (Beaman et al. 1962).

A common plant locally in east central Mexico but occurring from southern San Luis Potosí to Chiapas and inland to eastern Michoacán (Fig. 6). *Carex peucophila* occupies various habitats from roadsides, streambanks, and moist meadows

in oak, oak-pine, or pine forests to alpine meadows and has a very wide elevational range from (2000–) 2400–3800 (–3950) m. Fruiting occurs from early July through September, but perigynia are persistent on the culms for several months.

Additional Specimens Examined. Chiapas: Mt. Malé, near Porvenir, 6 Jul 1941, *Matuda 4632* (LL, mixed with *C. anisostachys*).—Distrito Federal: Delegación de Cuajimalpa, La Cienegilla, cerca del Cerro de San Miguel, 9 Aug 1967, *Cruz C. 1706* (ENCB); Delegación de Alvaro Obregón, 5 km al NE de Cuajimalpa, 11 Jul 1967, *Cruz C. 1750* (MICH); Delegación de Alvaro Obregón, 5 km al NE de Cuajimalpa, 21 Aug 1969, *Durán M. 46* (ENCB); Delegación de Cuajimalpa, Desierto de Los Leones, 5 Sep 1979, *González E. 1106* (CAS, VDB, WIS, XAL); vicinity of La Cima Railroad Station, on top of the Serjana de Ajusco, 19°07'N, 99°12'W, 14 Aug 1960, *Iltis et al. 933* (WIS); Llano de la Cieneguilla, cerca del cerro de la Palma, Sierra de las Cruces, 9 Jul 1967, *Rzedowski 23871* (US); Delegación de Tlalpan, alrededores de la estación La Cima, 8 Aug 1979, *Rzedowski 36176* (ENCB).—Hidalgo: Real del Monte, 12 Sep 1910, *Clokey 1694* (GH, UC), *Clokey 1698* (GH, UC); along Mineral del Monte-El Chico road ca. 2 km from Pachuca-Tampico hwy, 2 Aug 1987, *Freudenstein 2188* (MICH); El Chico Park, 2 Aug 1987, *Freudenstein 2189* (MICH); Mpio. El Chico, alrededores del Cerro de las Ventanas, 10 Jul 1979, *González E. 1055* (XAL); Mpio. Mineral del Monte, Real del Monte, near city of Pachuca, 27 Aug 1944, *Hernández X. 462* (MICH, MSC), *Hernández X. 465* (MICH, mixed with *C. vallicola* var. *hidalgensis* and *C. xalapensis*); 0.5 mi. N on Mex 105 from its jct with the road to Mineral del Monte, N of Pachuca. 19 Jul 1990, *Jones et al. 5521* (MICH, TAES); Mpio. Real del Monte, 1.5 km al WSW de Real del Monte, 16 Aug 1975, *Mendina C. 662* (MEXU); above Pueblo Nuevo and below Parque Nacional El Chico on road from Real del Monte to El Chico, 25 Jul 1948, *Moore & Wood 4104* (A, MICH); between Pachuca and Real del Monte, 19 Jul 1905, *Rose 8694* (NY, US); Cerro de las Ventanas, al N de Pachuca, 4 Aug 1963, *Rzedowski 17032* (ENCB); Mpio. Singuilucan, Cerro Cercano a El Ocote, 7 Sep 1963, *Rzedowski 17228* (ENCB); Cerro Ventoso, 5 km al NE de Pachuca sobre la carretera a Real del Monte, 20 Jun 1965, *Rzedowski 19965* (ENCB, MSC); Cerro de las Ventanas, 6 km al N de Pachuca, 28 Aug 1966, *Rzedowski 22999* (ENCB, MICH, MSC, WIS); *Rzedowski 23018* (ENCB, MSC); 25 Jun 1967, *Rzedowski 23823* (ENCB, MICH); Mpio. Epazoyucan, cerca de Peñas Largas, 3 Aug 1975, *Rzedowski 33429* (ENCB); Presa Jaramillo, 4 km al N de Pachuca, 29 Jul 1978, *Rzedowski 35752* (ENCB); Mpio. Epazoyucan, cerca de Peñas Largas, 22 Jul 1979, *Rzedowski 36227* (MEXU); Mpio. Epazoyucan, 1 km al S de El Guajolote, 22 Jul 1979, *Rzedowski 36238* (MEXU).—México: below Ojos de Agua, Nevado de Toluca, 11 Jul 1938, *Balls 5005* (K, US); Paso de Cortéz, 17 Sep 1958, *Beaman 2579* (GH, MSC); Tlaloc, near summit of mtn, 22 Aug 1958, *Beaman 2336* (MICH, MSC); Iztaccíhuatl, S side of mtn between La Joya and Altzomoni, 25 Mar 1961, *Beaman L-39* (MSC, chromosome voucher pressed from greenhouse material); 24 Jun 1962, *Beaman L-39–3* (MSC, pressed from greenhouse material); Mpio. Zoquiapán, Llano Grande, cerca de Río Frío, 16 Sep 1966, *Cruz C. 1280* (ENCB); Mpio. Tlalmanalco, Llanos La Cienega, vertiente NW del Ixtaccíhuatl, en región de Peñas Cuatos, 18 Jul 1982, *García P. 1631* (MICH); 1 km de Cahuacán, sobre la carretera a Villa del Carbón, Sep 1977, *González E. 991* (CAS, VDB); Mpio. Ixtapaluca, Llano Grande, cerca de Río Frío, 14 Oct 1979, *González E. 1135* (MEXU), *González E. 1136* (MEXU, VDB); Nevado de Toluca, 14 Aug 1964, *González Q. 1233* (ENCB); Mpio. Ixtapaluca, Estación Experimental de Investigación y Enseñanza de Zoquiapan, 8 km S de Río Frío, Llano de Aculco, 4 Jul 1975, *Koch 75282* (ENCB, MEXU); San Rafael Atlinco, Jul 1929, *Lyonnet 278* (MEXU, US); Nevado de Toluca, 19 Oct 1952, *Matuda 26602* (MEXU, NY); peak of Popocatépetl, 7–8 Aug 1901, *Rose 5994* (MICH, NY, US); Mpio. Nicholás Romero, 1 km al S de Cahuacán, 27 Jun 1963, *Rzedowski 16816* (ENCB); vertiente SW del Ixtaccíhuatl, 4 km al N de la Estación Retransmisora, 15 Aug 1965, *Rzedowski 20157* (DS, ENCB, MICH; all mixed sheets with *C. orizabae*); vertiente N del Nevado de Toluca, 6 Aug 1966, *Rzedowski 22873* (ENCB); 5 km al W del Paso de Cortés, vertiente NW del Popocatépetl, 9 Oct 1966, *Rzedowski 23252* (ENCB); Mpio. Villa Nicholás Romero, 2 km al SE de Cuhaucán, 11 Jun 1967, *Rzedowski 23814* (ENCB); Mpio. Texcoco, 8 km al E de Coatlinchán, 20 Jul 1967, *Rzedowski 24043* (MICH); Mpio. Iturbide, Palomas, 8 Aug 1968, *Rzedowski 25929* (DS, MICH; mixed with *C. curviculmis*); alrededores de La Presa Iturbide, 6 km al NNW de Santiago Tlazala, 7 Aug 1977, *Rzedowski 35101–A* (ENCB); 5 km al W de Progresso Industrial, sobre la carretera a Villa del Carbón, 18 Sep 1977, *Rzedowski 35280* (ENCB); Mpio. Naucalpan, Villa Alpina, 1 Jul 1979, *Rzedowski 36151* (ENCB).—Michoacán: Summit of Cerro San Andres, ca. 12 kms (straight line distance) N of Ciudad Hidalgo, 6 Sep 1960, *Beaman 4305* (MSC).—Oaxaca: 19 km NE of hwy 190 on road to Guelatao (hwy 175), just below "La Cumbre," 12–13 Oct 1983, *Anderson 13069* (ENCB, MEXU, MICH); along road through San Juan del Estado, 20 km from the Pan-Am hwy, 24 Jul 1987, *Freudenstein 2158* (MICH); near km 127 along Tuxtepec-Oaxaca Rd, 26 Jul 1987, *Freudenstein 2163* (MICH);

along hwy 175, 15.5 mi NE of Gelatao, 24 Dec 1975, *Reznicek & Gregory M-313* (MICH); Sierra de Zempoaltepetl, 2 km by road SW of El Carrizal, along road from Tlacolula to Yarganiza, ca. 37 km E of Oaxaca, 20 Feb 1988, *Reznicek 8067 & Reznicek* (MICH); Sierra de Juárez, along hwy 175, 15.5 km by road SW of Cerro Pelón, ca. 55 km NE of Oaxaca, 21 Feb 1988, *Reznicek 8074 & Reznicek* (MICH).—PUEBLA: Iztaccíhuatl, S side of mtn, 31 Jul 1958, *Beaman 1979* (MSC); Pico de Orizaba, SW side of mtn in cañada, 10 Sep 1958, *Beaman 2510* (GH, MEXU, MICH, MSC, NY, TEX, US, WIS); Campo experimental San Juan Tetla, 10 km al SW de San Martín Texmelucan, 20 Aug 1966, *May-Nah 2069* (ENCB, MSC); Arroyo Paso Buey, NW side of Volcán Pico de Orizaba and 7 km NW of the summit, 0.5 km SE of Miguel Hidalgo, 7 Sep 1986, *Nee & Soule 33020* (NY, WIS); Puenta del Emperador near La Venta, 18 Aug 1944, *Sharp 44433* (MO); Paso de Cortés, alrededor del monumento entre Ixctaccíhuatl y Popocatépetl, 28 Jun 1970, *Weber 368* (ENCB, MICH).—SAN LUIS POTOSÍ: 23.8 mi E on Mex 70 from its jct with Mex 57/80 in San Luis Potosí, SE of Altimira, 21 Jul 1990, *Jones et al. 5590* (MICH, TAES).—VERACRUZ: Cofre de Perote, NW side of mtn, 7 Aug 1958, *Beaman 2202* (MSC, mixed with *C. orizabae*); Mpio. Calcahualco, 4 km SW of Jacal, 19°06'N, 97°14'W, 6 Jul 1982 *Nee & Diggs 24776* (F, NY, WIS); Mpio. Perote, Cofre de Perote, by road at km 22 from Perote, 5 Sep 1976, *Pankhurst 76/136* (F).

Although a common plant locally, this species has had much too wide a Mexican range ascribed to it by past authors. Hermann (1974) noted it from "Baja California and Durango to Guatemala," but the Baja and Durango plants are here referred to *C. lagunensis*. As well, high elevation collections with narrow perigynia are here described as *C. curviculmis*. As here circumscribed, *C. peucophila* is restricted to east-central and southern Mexico, south very locally at higher elevations to Guatemala, and comprises small plants with short-creeping rhizomes, usually lax and flexuous culms, and few, small, spikes of relatively short perigynia (3.3–) 3.5–4.4 (–4.7) mm long and 1.8–2.4 (–2.6) times as long as wide, with short beaks 0.6–1.2 (–1.5) mm long. The Chiapas specimen (Mt. Malé, *Matuda 4632*) is too immature for certain determination, but is assigned to *C. peucophila* because Mt. Malé barely attains 3000 m, the lower elevational limit of *C. curviculmis*, the only other species to which the specimen could be referred.

The other two ± widespread species with short inflorescences and reddish brown pistillate scales that occur in Mexico, *C. curviculmis* and *C. lagunensis*, are often mistaken for *C. peucophila*. They differ significantly in perigynium size and proportions, as shown in Fig. 7.

Although *C. peucophila* occurs over an extremely wide altitudinal range, there seem to be no essential differences between plants of lower elevations and plants from the highest elevations, except that the high-elevation plants tend to be more compact, especially when growing in exposed habitats. Some collections from lower elevations, especially those growing in deep shade, can be very depauperate, with only a few, small, narrow perigynia per spike. These can be almost impossible to key properly. The report of *C. deweyana* Schwein. from Mexico (Cochrane 1981) was based on one of these depauperate specimens, *Hernández X. 462* (MSC). *Carex deweyana* should be deleted from the Mexican sedge flora.

Kükenthal (1909) united *Carex peucophila* with the Andean South American *C. mandoniana* Boeck. (under the name *C. pinetorum* Liebm.). Some high elevation Andean plants do appear to be identical with *C. peucophila*, but the type of *C. mandoniana* (Bolivia, Prov. Larecaja, viciniis Sorata, Nov 1858–Apr 1859, *Mandon 1429*; holotype: B, destroyed; isotypes: GH! K! MICH! NY-3 sheets! P!) is not. It has very narrow achenes ca. 1 mm or less wide and small perigynia that are scarcely winged and only sparsely serrulate-margined on the beak and uppermost part of the body, and appears to belong to the C. *bonplandii* complex. A great deal more work is needed on South American members of section *Ovales* before their systematics can be resolved.

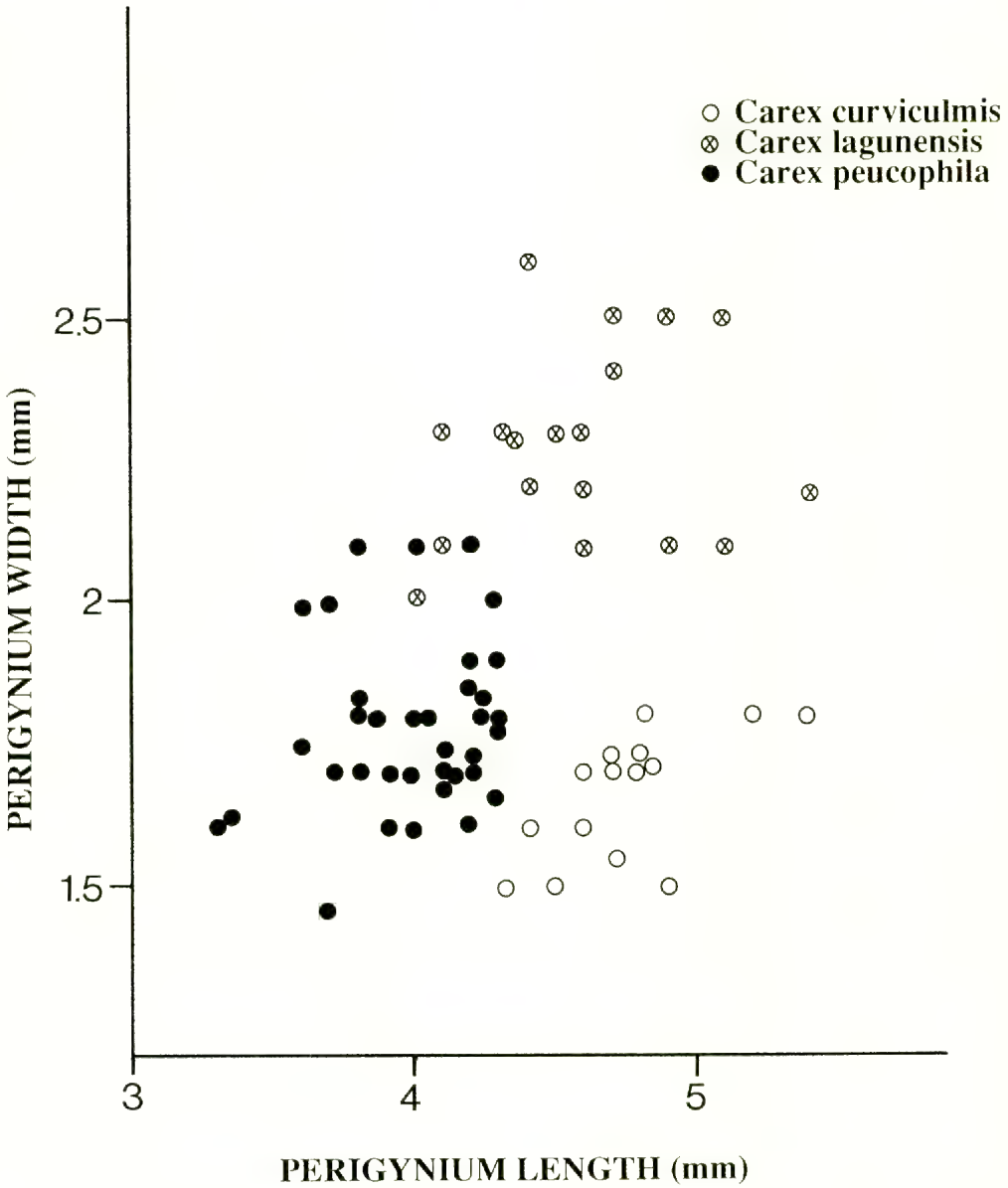

FIG. 7. Scatter plot of perigynium length and perigynium width for *Carex curviculmis*, *C. lagunensis*, and *C. peucophila*.

11. Carex subfusca W. Boott in S. Watson, Bot. S. Calif. 2: 234. 1880.—TYPE: U.S.A. California: Lake Tahoe, Bear Valley, *Kellogg s.n.* (lectotype, here designated: GH!). Figs. 11, 2k.

Densely cespitose in small clumps; fertile culms 15–90 cm tall, erect, trigonous, smooth except sometimes just below inflorescence, where finely scabrous; bladeless basal sheaths pale brown, ± persistent. Leaves 4–8, on the lower 1/10–2/5 of the culm; blades 3–30 cm long, 1.2–3.5 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 1.5–9.5 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish

hyaline, prolonged up to 3.5 mm beyond the leaf bases, the apex shallowly concave to convex-prolonged, whitish hyaline; ligules 1.4–6 mm long, rounded, the free portion entire, up to 0.4 mm long. Vegetative culms ca. 3–12 cm tall with ca. 6–8 leaves; leaves tristichous and mostly clustered in the upper 1/2 of the culm. Inflorescences 1.1–2.2 (–2.8) cm long, in an ovoid head, the upper spikes overlapping, the lowest two spikes 1.2–5 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or rarely setaceous, 0.4–1 (–3.5) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes (3–) 5–9, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 6–11 mm long, pistillate portion 5–9 mm long, 4–6 mm wide, ca. 10–40-flowered, staminate portion 1–3.5 mm long, ca. 1.5–2 mm wide, ca. 1–8-flowered. Pistillate scales 2.1–3.9 mm long, 1.3–1.7 mm wide, ovate, acute, yellowish brown to reddish brown with a narrow green center and hyaline margins, 1-nerved. Staminate scales 2.2–3.9 mm long, 1.4–2 mm wide, ovate, acute to acuminate, pale yellowish brown to reddish brown with a narrow green center and hyaline margins, 1-nerved. Perigynia 2.7–4.1 mm long, 1.2–1.7 mm wide, 1.9–2.6 times as long as wide, spreading-ascending, plano-convex with ovate bodies 1.8–2.7 mm long, (1.2–) 1.4–1.8 times as long as wide and (1.6–) 1.9–2.5 times as long as the beak, widest 0.8–1.3 mm above base, narrowly winged and serrulate-margined above the widest point, contracted into a beak, green to pale brown, glabrous, sessile, adaxial side (0–) 3–7-nerved over achene, abaxial side 3–11-nerved over achene; beaks 0.9–1.3 mm long, flattened and serrulate-margined but with the apical 0.2–0.4 mm terete and smooth, the apex obliquely erose. Achenes 1.1–1.7 mm long, 0.9–1.1 (–1.2) mm wide, 1.1–1.5 times as long as wide, biconvex, ovate-oblong, pale brown, short-stipitate; style straight; stigmas 2. Anthers 3, 1.3–2.6 mm long. Chromosome number: $n = 42$ (Whitkus 1991).

A common (or at least commonly collected) species of wet meadows, seepy or seasonally moist slopes and rocky banks, streambanks, and lakeshores at 1600–2700 m in the Sierra San Pedro Mártir and the Sierra de Juárez of northern Baja California (Fig. 6). Fruiting specimens have been collected from May through September.

Additional Specimens Examined. Baja California Norte: Sierra San Pedro Mártir, head of Cañada el Copal and S slope of Cerro Venado Blanco, 3 Jun 1988, *Boyd 2313 et al.* (F, RSA); Sierra San Pedro Mártir, saddle at SW end of Cerro Venado Blanco, 17 Jul 1988, *Boyd 2600 et al.* (F, RSA); Sierra San Pedro Mártir, Yerba Buena, 31°00'N, 115°27'W, 16 Aug 1967, *Moran & Thorne 14179* (SD, WIS); Sierra San Pedro Mártir, Los Llanitos, 30°58'N, 115°26'W, 17 Aug 1967, *Moran & Thorne 14277* (SD); Sierra San Pedro Mártir, La Encantada, 30°55'N, 115°24'W, 19 Aug 1967, *Moran & Thorne 14344* (RSA, SD); Sierra San Pedro Mártir, La Concepción, 31°01'N, 115°37'W, 31 May 1968, *Moran 15045* (RSA, SD); Sierra San Pedro Mártir, above Yerba Buena, 31°02'N, 115°27'W, 30 May 1977, *Moran 24201* (SD); Sierra San Pedro Mártir, Arroyo La Grulla, 5 km SW of La Grulla, 30°51 1/2'N, 115°31'W, 10 Aug 1977, *Moran 24475* (ARIZ, RSA, SD), *Moran 24483* (SD); Sierra San Pedro Mártir, ca. 3 km NW of Los Llanitos, 30°59'N, 115°26 1/2'W, 3 Sep 1979, *Moran 28011* (SD); Sierra San Pedro Mártir, near stream below La Grulla, 30°53 1/2'N, 115°29'W, 8 Jun 1982, *Moran 30928* (MICH, MSC); Sierra San Pedro Mártir, E of Vallecitos, 30°00 1/2'N, 115°27'W, 2 Jul 1982, *Moran 30986* (SD); upper San Jose Creek bottom, 0–3 mi beyond end of road into N end of high Sierra San Pedro Mártir, 7 Jun 1962, *Olmsted 4570* (RSA); left-hand fork of SSE tributary of Río San Rafael, N end of high Sierra San Pedro Mártir, 7 Jun 1962, *Olmsted 4627* (RSA); below upper end of road from San José (Melling) Ranch and oak pasture below Prado del Corona in central Sierra San Pedro Mártir, 10 Jun 1962, *Olmsted 4759* (RSA); Sierra San Pedro Mártir, along Arroyo Rancho Viejo, 6 miles by road S of Vallecitos Meadow, 31°57'30"N, 115°25'W, 18 Jun 1988, *Sanders 7975 et al.* (RSA); Sierra de Juárez, Laguna Hansen (Laguna Juárez), 32°04'22"N, 115°54'13"W, 13 Jul 1987, *Tallent 744* (MICH), *Tallent 745* (MICH); Sierra de Juárez, Constitución National Park, N end of Laguna Hansen, 28 May 1983, *Thorne 55727 et al.* (RSA, SD); E margin of

Laguna Hansen, 28 May 1983, *Thorne 55892 et al.* (RSA, SD); Sierra San Pedro Mártir Nat'l Park, upper Vallecitos meadows, 30°01'N, 115°28'W, 18 Sep 1983, *Thorne 57229 et al.* (RSA); Vallecitos, 30°01'N, 115°28'W, 18 Jun 1985, *Thorne 60822 et al.* (RSA); Parque Nacional San Pedro Mártir, N of Vallecitos, 30°02'N, 115°28'W, 19 Jun 1985, *Thorne 60945 et al.* (RSA); Sierra San Pedro Mártir, 31°02'N, 115°28'W, 7 May 1986, *Thorne 61983 et al.* (RSA); Sierra de Juárez, Parque Nacional Constitución de 1857, Laguna Hansen, 26 May 1987, *Thorne 62388 et al.* (RSA); Sierra San Pedro Mártir, La Encantada, 22 Sep 1930, *Wiggins & Demaree 5004* (GH, POM); about 1 mile SW of Observatory gate, on graded road from San Telmo, 31°01'40"N, 115°29'20"W, 29 May 1982, *Yatskievych 82–192 et al.* (ARIZ).

Carex subfusca has small, narrowly winged perigynia 2.7–4.1 mm long, 1.2–1.7 mm wide, with ovate bodies and terete beak apices that are unlike those of any other species of section *Ovales* in Mexico. The pistillate scales in this species are occasionally large enough to essentially cover the perigynia. It is confined to northern Baja and coexists with no other species except *C. athrostachya*, which is also confined to Baja. *Carex subfusca* is wide ranging in the western United States from Washington to Idaho and south to California and New Mexico; apparently it also occurs in Hawaii (Krauss 1950). The description above has been drawn exclusively from the ample Baja material. The relationships of *C. subfusca* to the other members of the *C. pachystachya* complex are discussed by Whitkus (1992).

12. Carex tolucensis (F. J. Hermann) Reznicek, comb. nov., *Carex subbracteata* var. *tolucensis* F. J. Hermann, Brittonia 23: 145. 1971.—TYPE: MEXICO. México: 27 km SW of Toluca on road to Temascaltepec, 9 Jul 1964, *Mick & Roe 236* (holotype: MICH!; isotype: WIS!). Figs. 1m, 2l.

Cespitose in small clumps; fertile culms ca. 50–90 cm tall, erect, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, persistent. Leaves 3–4, on the lower 1/5–1/3 of the culm; blades 3–30 cm long, 1.5–3 mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 3–8 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, not prolonged beyond the leaf bases, the apex concave, whitish hyaline; ligules 0.8–2.5 mm long, rounded, the free portion entire, up to 0.2 mm long. Vegetative culms unknown. Inflorescences ca. 1.7–2 cm long, in a dense narrow head, the upper spikes overlapping, the lowest two spikes ca. 3–6 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or rarely setaceous, 0.4–1.2 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes ca. 5–6, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, ovoid, 6–9.5 mm long, pistillate portion 5–7.5 mm long, 5–7 mm wide, ca. 15–30-flowered, staminate portion 1–2 mm long, appressed against the base of the pistillate portion, ca. 3–7-flowered. Pistillate scales 3.2–3.9 mm long, 1.5–2.2 mm wide, narrowly ovate, obtuse to acute, reddish brown with a narrow green center, 1-nerved. Staminate scales 2.8–3.6 mm long, 1.6–2 mm wide, ovate, acute to acuminate, reddish brown with a narrow green center, 1-nerved. Perigynia ca. 4.2–4.9 mm long, (1.8–) 2–2.4 mm wide, 1.9–2.3 times as long as wide, appressed, plano-convex with elliptic to ± suborbicular (sometimes somewhat asymmetrical) bodies ca. 3–3.3 mm long, 1.3–1.6 times as long as wide and 1.9–2.4 times as long as the beak, widest 1.4–1.7 mm above base, narrowly and thickly winged and serrulate-margined above widest point, contracted into a beak, green to pale brown, glabrous, sessile, adaxial side nerveless or faintly 1–3-nerved over achene, abaxial side faintly (0–) 3–7-nerved over achene; beaks 1.3–

1.6 mm long, flattened and serrulate-margined but with the apical 0.4–0.6 mm terete and smooth, the apex obliquely erose. Achenes ca. 1.9–2 mm long, 1.4–1.6 mm wide, ca. 1.2–1.4 times as long as wide, biconvex, broadly obovate, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, ca. 1.2–1.5 mm long. Chromosome number unknown.

Known only from the type, collected near the Nevado de Toluca, State of México (Fig. 6), at 2800 m on a steep, west-facing slope dominated by *Pinus* and *Abies* with a tussock grass understory. Fruiting in July, so far as known.

This plant is raised to species rank because its resemblance to *Carex subbracteata* Mack. of low to moderate (up to about 1500 m) elevations in the California Coast Ranges seems only to be superficial. The inflorescences and overall habit of these two species are indeed relatively similar. The perigynia and achenes, however, are quite different. *Carex tolucensis* has appressed-ascending perigynia 2–2.4 mm wide and ca. 1.9–2.3 times as long as wide with achenes 1.4–1.6 mm wide. *Carex subbracteata* has spreading-ascending perigynia 1.5–1.8 mm wide and ca. 2.3–3.1 times as long as wide with achenes 1.2–1.4 mm wide. As noted by Hermann (1971), the perigynia of *C. tolucensis* are also more abruptly contracted to a beak than those of *C. subbracteata*. Except for the quite distinctive *C. wootonii*, *C. tolucensis* is unique among Mexican members of section *Ovales* in combining perigynia greater than 2 mm wide and conspicuous terete, smooth beak apices.

13. Carex tribuloides Wahlenberg, Kongl. Vetensk. Acad. Nya Handl. 24: 145. 1803.—TYPE: America boreali, *Kalm s.n.* Efforts by Moberg and Nilsson (1990) to locate the type were unsuccessful. Figs. 1n, 2m.

Cespitose in small clumps; fertile culms (25–) 40–110 cm tall, erect, trigonous, smooth except just below inflorescence, where finely scabrous; bladeless basal sheaths brown, ± persistent. Leaves 7–10, on the lower 3/5–3/4 of the culm; blades 5–25 cm long, 2–5.5 (–7) mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 2.5–9 cm long, somewhat loosely enveloping culms and ± wing-angled, glabrous, green; the inner band of sheaths glabrous, green with at most a very short, rapidly tapering hyaline zone at the apex (the lower sheaths sometimes with a longer hyaline zone), not prolonged beyond the leaf bases, the apex concave, whitish hyaline; ligules 4–12 mm long, rounded, the free portion entire to ± erose, up to 1.1 mm long. Vegetative culms ca. 25–70 cm tall, annual or sometimes perennating and rooting at the nodes if contacting the soil, leaves ca. 14–25, tristichous and mostly loosely clustered in the upper 1/2 of the culm. Inflorescences (1.9–) 2.3–7 cm long, the upper spikes overlapping, the lowest two spikes 3–15 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.5–2.5 (–4.5) cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes (3–) 5–13, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, clavate-obovoid to ± turbinate, 6–16.5 mm long, pistillate portion 4.5–12 mm long, 5–9.5 mm wide, ca. (20–) 25–90-flowered, staminate portion 0.5–2 (–6) mm long, ca. 1.5 mm wide, ca. 1–4 (–9)-flowered. Pistillate scales 1.9–3 mm long, 0.6–1.3 mm wide, narrowly ovate, acute to acuminate, whitish hyaline to pale silvery brown with a green center, 1-nerved. Staminate scales ca. 2.4–3.8 mm long, ca. 0.8–1.3 mm wide, narrowly ovate, acute to acuminate, whitish hyaline to pale silvery brown with a green center, 1-nerved. Perigynia 2.8–5.2 mm long, 0.9–1.5 (–1.7) mm wide, (2.3–) 2.7–4 (–5) times as long as wide, appressed-ascending to ascending,

biconvex and very thin and scalelike except where distended by the achene, with narrowly ovate to lanceolate or oblanceolate (usually somewhat asymmetrical) bodies 1.9–3.6 mm long, 1.8– 3 (–4) times as long as wide, and 1.9–4 times as long as the beak, widest ca. 1.3–2.3 mm above base, narrowly thin-winged and serrulate-margined above widest point, gradually tapered into the beak, green to pale brown, glabrous, sessile, adaxial side 3–7-nerved over achene, abaxial side 5–9-nerved over achene; beaks 0.8–1.4 mm long, strongly flattened and serrulate-margined to apex, the apex bidentulate with scabrous-margined teeth up to 0.5 mm long. Achenes 1.2–1.6 mm long, 0.6–0.8 mm wide, (1.5–) 1.8–2.3 times as long as wide, biconvex, narrowly ovate-oblong, pale brown, short-stipitate; style nearly straight to slightly sinuous; stigmas 2. Anthers 3, 1.1–2 mm long. Chromosome number: $n = 35$ (Moore & Calder 1964; Wahl 1940).

A rare plant of moist, broad-leaved forests at ca. 1200–1400 m; collected only in the vicinity of Xalapa, Veracruz (Fig. 6). Fruiting in April and May, so far as known.

Specimens Examined. Veracruz: 3 km al W de Xalapa, 8 May 1973, *Acosta & Dorantes 251* (ENCB); near Jalapa, 27 Apr 1899, *Pringle 7802* (GH, US).

Carex tribuloides ranges from Minnesota to southwestern Quebec and south to eastern Texas and northern Florida. The Mexican stations are quite disjunct, but the moist Mexican montane forests contain several disjunct occurrences of eastern deciduous forest *Carex* species, including *C. albicans* var. *australis* (L. H. Bailey) Rettig (*C. physorhyncha* Steud.), *C. bromoides* Willd. subsp. *bromoides*, *C. laxiflora* var. *serrulata* F. J. Herm., *C. lurida* Wahlenb., and *C. nigromarginata* Schwein.

Carex tribuloides is the widest leaved member of section *Ovales* in Mexico, with leaves up to at least 5.5 mm wide. The combination of narrow perigynia 0.9–1.5 (–1.7) mm wide and herbaceous, green inner bands to the sheaths is unique among Mexican species of section *Ovales*. It shares with *C. longii*, a close relative, well-developed, leafy, and elongate vegetative culms that can perennate and function in vegetative reproduction (Reznicek & Catling 1986). No other Mexican species are known to have this feature, although vegetative culms are unknown or poorly known in several species. *Carex tribuloides* also has quite leafy fertile culms, with the leaves extending 3/5–3/4 of the way up the culm. Only *C. longii*, with leaves extending (1/4–) 1/3–3/5 of the way up the culm, approaches this leafiness. Except for the enigmatic *C. interjecta*, all other Mexican species have the leaves nearly basal or only on the lower 1/3 of the culm.

Carex tribuloides is quite a variable species. Collections from the northern portions of the species range have long, narrow perigynia ca. 3.5–5.2 mm long and 3–4 (–5) times as long as wide, large spikes in ± dense, stiff inflorescences, and quite wide leaves. Plants from the south of its range in the United States, especially from the Mississippi embayment and the western Gulf coastal plain, tend to have shorter, wider perigynia ca. 2.8–4.5 mm long and (2.3–) 2.7–3.2 times as long as wide, smaller spikes often in looser inflorescences, and generally narrower leaves. The southern plants were segregated by Mackenzie (1931) as var. *sangamonensis* Clokey, but whether or not this variation is really discontinuous and worthy of taxonomic recognition is uncertain and requires more study. The two Mexican collections of *C. tribuloides* are similar to the southern United States forms, but the description above includes the entire variation of the species.

14. Carex wootonii Mackenzie, Smithsonian Misc. Collect. 65(7): 1. 1915.—TYPE: U.S.A. New Mexico: San Francisco Mountains, 15 Jul 1892, *Wooton s.n.* (holotype: NMC!). Figs. 1o, 2n.

Carex egglestonii var. *festivelliformis* F. J. Hermann, Brittonia 12: 78. 1960.—TYPE: MEXICO. Nuevo León: Mpio. Galeana, near peak of Cerro Potosí, 25 Jul 1938, [*Schneider*] *954* (holotype: MICH!; isotypes: F! GH! ILL! MO! NY! US!).

Densely cespitose in small clumps; fertile culms 25–70 cm tall, stiffly erect, trigonous, finely scabrous-angled; bladeless basal sheaths pale brown, ± persistent. Leaves 3–5, on the lower 1/8–1/4 of the culm; blades 5–35 cm long, 1.8–3.8 (–4.5) mm wide, plicate, glabrous, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 4– 8 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline to pale brown, usually prolonged up to 0.9 mm beyond the leaf bases, the apex concave, whitish hyaline; ligules 1.5–2.9 mm long, rounded, the free portion entire, up to 0.4 mm long. Vegetative culms poorly known, ca. 3–12 cm long, leaves ca. 6–10, mostly clustered in the upper 1/3 of the culm. Inflorescences 1.8–5 cm long, elongate, the upper spikes overlapping, the lowest two spikes 3–16 mm distant, spikes single at nodes, sessile, lowermost bracts scalelike or sometimes setaceous, 0.7–6 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 3–6, gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, clavate-ovoid, 7–21 mm long, pistillate portion 9–14 mm long, 4.5–9 mm wide, ca. 8–30-flowered, staminate portion 1.5–9 mm long, ca. 1.5–2 mm wide, ca. 1–8-flowered. Pistillate scales 3.8–6.6 mm long, 1.6–2.2 mm wide, narrowly ovate, acute, dark reddish brown with a narrow green center and wide hyaline margins, 1-nerved. Staminate scales 3.9–8.2 mm long, 1.5–2.1 mm wide, lanceolate to narrowly ovate, acute to acuminate, dark reddish brown with a narrow green center and hyaline margins, 1-nerved. Perigynia (5.2–) 5.5–7.5 mm long, 2.1–3 mm wide, ca. (2–) 2.2–3.1 times as long as wide, ascending, plano-convex with narrowly ovate to ovate bodies ca. 4–4.8 mm long, ca. 1.6–2 times as long as wide and 1.7–2.9 times as long as the beak, widest ca. 2–2.6 mm above base, broadly winged and serrulate-margined except near base, gradually tapered into a beak, green to pale brown, glabrous, sessile, essentially nerveless over achene on both faces; beaks 1.4–2.4 mm long, strongly flattened and serrulate-margined but often with the apical 0.1–0.4 mm terete, ± hyaline, and smooth, the apex bidentate with scabrous-margined teeth up to 0.6 mm long. Achenes 1.9–2.7 mm long, 1.4–1.6 (–2.1) mm wide, (1.1–) 1.4–1.9 times as long as wide, biconvex, ovate-oblong, pale brown, short-stipitate; style essentially straight; stigmas 2. Anthers 3, 2.2–3.5 mm long. Chromosome number unknown.

An uncommon species occurring from Coahuila and Nuevo León south to Durango (Fig. 6) in dry to mesic meadows and clearings in pine forest at 2500–3600 m. Fruiting in July and August.

ADDITIONAL SPECIMENS EXAMINED. COAHUILA: Sierra Madre del Carmen, Campo El Tres, 29°00'N, 102°36'W, 5 Aug 1974, *Wendt & Adamcewicz 491* (ENCB, LL, MEXU, TEX).—DURANGO: Mpio. Pueblo Nuevo, 7 km al W de El Salto, 21 Aug 1981, *González E. & Rzedowski 1925* (ENCB).

This is the first Mexican report of this species, previously known from Arizona and New Mexico. It is distinctive among Mexican members of section *Ovales*

in having the largest perigynia, (5.2–) 5.5–7.5 mm long. Hermann (1960) described his *Carex egglestonii* var. *festivelliformis* with the Cerro Potosí specimen of *C. wootonii* as the type, but his concept was also based on *Pringle 1402*, here described as *C. festivelloides*. The combination of characters from the mixing of these two species (one of which was indeed undescribed) probably prevented him from recognizing *C. wootonii* in Mexico. *Carex egglestonii* differs from *C. wootonii* in having the spikes in dense, ovoid heads, and in having the beak uniformly flattened and serrulate to the apex. *Carex wootonii* relatively frequently has elongate lower inflorescence bracts like those of *C. athrostachya* and *C. festivelloides*. Besides *C. egglestonii* var. *festivelliformis*, the Schneider collection from Cerro Potosí has been reported as *C. orizabae* by Beaman and Andresen (1966) and McDonald (1990) and as *C. peucophila* by García-Arevalo and González-Elizondo (1991).

The Durango specimen (*González E. & Rzedowski 1925*) is somewhat disjunct and is placed with *C. wootonii* with some hesitation. In its overall aspect, and perigynium size and shape, it is a good match for *C. wootonii*. The inflorescence, however, is more compact than is usual for *C. wootonii*, and the achenes are much wider, ca. 1.9–2.1 mm wide and only 1.1–1.2 times as long as wide. *Carex wootonii* otherwise has achenes ca. 1.4–1.6 mm wide and 1.4–1.9 times as long as wide. The local California endemic *C. davyi* Mack. has large, wide perigynia like those of *C. wootonii* but more compact heads. It too, however, differs from the Durango plant in its narrower achenes, as well as having the perigynia strongly nerved over the achene adaxially. More material is needed to determine the constancy and significance of this variation, but this plant may well be a distinct entity.

EXCLUDED NAMES

Carex bonplandii Kunth, Enum. Pl. 2: 380. 1837.—TYPE: America meridionalis, *Bonpland s.n.* (holotype: P!; isotype: P!). Mackenzie (1931) reported this species from Veracruz, presumably on the basis of the type of *C. orizabae*, since he placed that species in the synonymy of *C. bonplandii*. Hermann (1974) reported *C. bonplandii* from Oaxaca, "Sierra de San Filipe [sic], 10,000 ft," but that specimen (*Pringle 5723*) is here referred to *C. orizabae*. *Carex bonplandii* apparently does not occur as far north as Mexico.

Carex festivella Mackenzie, Bull. Torrey Bot. Club. 42: 609. 1915.—TYPE: U.S.A. Wyoming: Albany Co., Centennial Valley, 7 Jul 1897, *A. Nelson 3275* (holotype: NY; isotypes: GH, MICH-fragment ex herb. F. J. Hermann!). The Mexican specimen referred by Mackenzie (1915, 1931) to this species is here described as *C. festivelloides*. *Carex festivella* was also reported for Cerro Tancítaro by Leavenworth (1946), but the specimen supporting that report, *Leavenworth & Hoogstral 1171*, is *C. orizabae*. Whitkus and Packer (1984) submerge *C. festivella* under a broad concept of *C. microptera*.

Carex oreades C. A. Meyer ex Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9: 248. 1842, nomen nudum.

Carex purdiei Boott, Ill. Carex 1: 26. pl. 67. 1858.—TYPE: COLOMBIA. Bogs near the snow, Nevada de St. Martha, Jul 1844, *Purdie s.n.* (lectotype, here designated: K!). The single Mexican specimen tentatively referred to this species was redetermined as *C. echinata* Murray subsp. *townsendii* (Mack.) Reznicek; see Reznicek (1990).

Carex xerantica L. H. Bailey, Bot. Gaz. 17: 151. 1892.—TYPE: CANADA. [Saskatchewan]: File Hills, 4 Jul 1879, *Macoun s.n.* (syntype: BH); Moose Jaw, 18 Jul 1880, *Macoun s.n.* (syntype: BH). The two Mexican specimens referred to this species by Hermann (1974) are *C. lagunensis*.

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CAREX TOVARENSIS (CYPERACEAE), A NEW SPECIES FROM VENEZUELA

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Study of herbarium specimens from Venezuela previously considered to belong to the North American species *Carex virescens* Willd. disclosed that they represented a distinct species and a new local Venezuelan endemic.

Carex tovarensis Reznicek & G. A. Wheeler, sp. nov.—TYPE: VENEZUELA. Distrito Federal: Parque Nacional El Avila, ridgetop in vicinity of "Lagunazo," between Pico El Avila and Pico Occidental, above the city of Caracas, subpáramo vegetation of low shrubs and grassy areas, with much *Pteridium caudatum* and evidence of fire, clumps in damp area, 2200 m, 21 Jul 1979, *Nee & Whalen 16809* (holotype: F!; isotype: WIS!). Fig. 1.

Plantae cespitosae; culmi (6–) 15–60 (–75) cm alti; vaginae basales purpurascentes, glabrae vel pilosae. Folia 6–10, plerumque basalia; laminae 8–35 cm longae, 1.6–5.2 cm latae; vaginae (0.7–) 4.2–9.5 cm longae, glabrae vel pilosae, infimae purpurascentes; ligulae 1.8–5.6 mm longae. Inflorescentiae 1.2–6.5 cm longae; spicae plus minusve erectae; spica terminalis gynaecandra, spicae laterales pistillatae; bracteae infimae laminis (0.5–) 1.6–9 cm longis, (0.3–) 0.7–2.4 mm latis, evaginatis. Perigynia 1.9–2.6 mm longa, 0.9–1.4 mm lata, ascendentia, trigona, viridia, erostrata. Achenium 1.4–2 mm longum, 0.8–1.1 mm latum. Styli marcescentes; stigmata 3. Antherae 3, ca 0.9–1.1 mm longae.

Plants cespitose with short rhizomes; roots pale brown; fertile culms (6–) 15–60 (–75) cm tall, ± stiffly erect, trigonous, smooth or sparsely antrorsely scabrous below inflorescence, with glabrous to sparsely pilose, strongly reddish purple and sometimes sparingly fibrillose bladeless basal sheaths. Leaves 6–10, all but the upper 1–2 basal; blades 8–35 cm long, 1.6–5.2 cm wide, plicate, sparsely pilose adaxially above ligule and abaxially, the margins smooth proximally, finely antrorsely scabrous distally, the widest leaves 2.3–5.2 mm wide; leaf sheaths (0.7–) 4.2–9.5 cm long, ± glabrous to pilose, the lowermost strongly reddish purple tinged near base; inner band of sheaths stramineous to pale brown, pilose, especially on lower sheaths, to glabrous, ± red-dotted, the apex shallowly concave, slightly thickened, often finely short ciliate; ligules 1.8–5.6 mm long, rounded to acute, the free portion stramineous to pale brown, often sparsely ciliate with long hairs. Vegetative shoots ca 15–28 cm tall; leaves 7–9, ± similar to those of fertile culms; pseudoculms 2.5–6.5 cm long. Inflorescences 1.2–6.5 cm long, with the

spikes usually all strongly overlapping, the lowest two 0.2–1.3 (–2.9) cm distant; spikes single at nodes, erect to ascending, with the upper sessile and the lower on stiff, ± smooth peduncles 0.6–9.5 mm long; lowermost bracts with blades (0.5–) 1.6–9 cm long, (0.3–) 0.7–2.4 mm wide, sheathless, the upper bracts much reduced. Spikes 3–5, the terminal gynaecandrous, the lateral pistillate. Terminal spikes 8–20.5 mm long; staminate portion 3–10.5 mm long, 0.8–1.6 mm wide, ca 4–20-flowered; pistillate portion 5–13 mm long, 3–5.2 mm wide, ca 8–60-flowered; peduncles 1.5–3.8 mm long. Lateral spikes 4–21 mm long, 3.5–5 mm wide, ca 8–75-flowered, occasionally with a small secondary spike up to 5 mm long at base. Pistillate scales 1.4–2.7 (–3.9) mm long, 0.9–1.3 mm wide, obovate, acute to acuminate-awned, with an awn up to 0.9 (–2.4) mm long, the upper margins ± finely ciliate, hyaline with a green center, 3-nerved. Staminate scales 2–3 mm long, 1–1.4 mm wide, narrowly obovate, obtuse to acuminate, the upper margins ciliate, hyaline with a green center, 3-nerved. Perigynia 1.9–2.6 mm long, 0.9–1.4 mm wide, appressed-ascending, trigonous with ± flat, rhombic-elliptic faces, green, sparsely pilose at least in the distal two-thirds, strongly red-dotted, essentially sessile, 2–5-nerved, tapering to a ± incurved, truncate, hyaline orifice. Achenes 1.4–2 mm long, 0.8–1.1 mm wide, trigonous with ± flat to slightly concave, elliptic to obovate sides, ± loosely enveloped by the perigynia, stamineous to pale brown with ± blunt yellowish angles, ± sessile. Styles withering; stigmas 3. Anthers 3, ca 0.9–1.1 mm long.

Known only from the coastal range of northern Venezuela, where it occurs from 2000 to 2300 m in moist sites in areas dominated by low shrubs and grasses (subpáramo vegetation). Specimens in ripe fruit have been collected essentially throughout the year.

Additional Specimens Examined. **Venezuela.** Aragua: Prope Coloniam Tovar, 1854-5, *Fendler 1604*, (GH, K, US); Colonia Tovar and vicinity, 21 Mar 1921, *Pittier 9306* (GH, MICH, NY, US); Colonia Tovar, 21 Oct 1926, *Woronow 7195* (LE).—Distrito Federal: Lagunazo, 1865, *Moritz* (BM-2 sheets); Lagomazo, Colonia Tovar, 22 Dec 1915, *John 435* (US); Silla de Caracas, Coastal Range, La Cienega, 26-29 Dec, 1918 *Pittier 8310* (US); La Cienega, 1939, *Vogl 1009* (NY); Silla de Caracas, 15 Feb 1969, *Baruch 28* (NY); El Avila, Lagunazo, 31 Jul 1976, *Manara s.n.* (NY).

Carex tovarensis is the second South American species referred to *Carex* section *Porocystis* Dumort. (section *Virescentes*). The epithet refers to Colonia Tovar in the state of Aragua, the general collecting locality for many of the specimens.

Previous authors, starting with Boott (1858), knew of these Venezuelan plants, but did not consider them distinct from the North American *Carex virescens*. Kükenthal (1909) referred them to *C. virescens* var. *costata* (Schwein.) Dewey, as did Steyermark and Huber (1978). However, the type of *C. virescens* var. *costata* is from Pennsylvania, and the name is a synonym of *C. virescens* (Mackenzie 1935). Mackenzie (1935, pg. 322) considered the Venezuelan *Carex virescens*-like plants to be "a closely allied but distinct species," but no name for it has heretofore been validly published, although Mackenzie annotated several herbarium sheets with the name "*C. phyllopoda* Mackenzie." The name *Carex phyllopoda* was also used, as a nomen nudum, by Knuth (1926), who reported *Pittier 9306* under this name (and *Fendler 1604* under the name *C. virescens* var. *costata*!).

Carex tovarensis differs from *C. virescens* by having shorter anthers ca 0.9–1.1 mm long, strongly red-dotted perigynia, less pubescent leaves, especially distally,

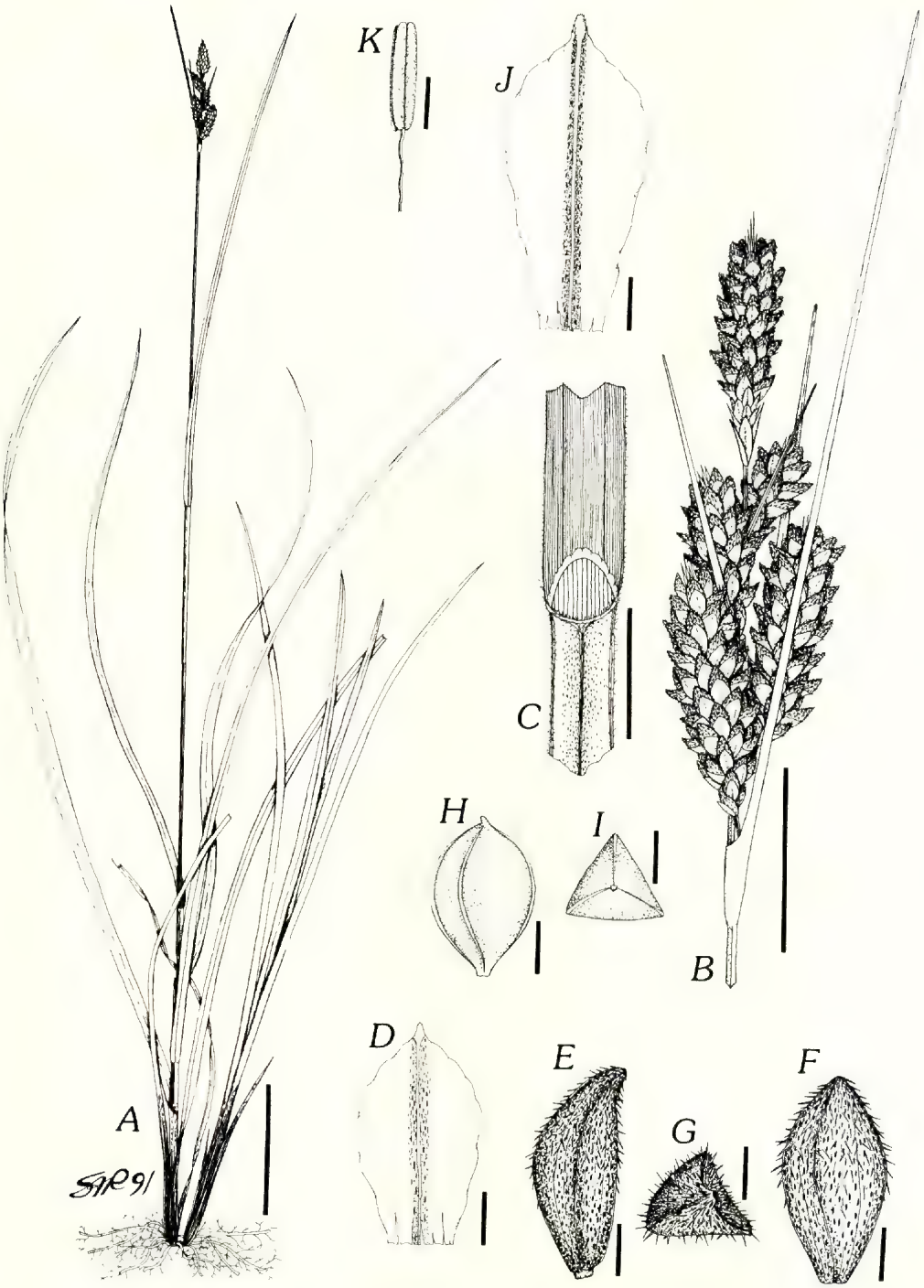

FIG. 1. *Carex tovarensis*. A. Habit. B. Portion of inflorescence. C. Sheath and ligule. D. Pistillate scale. E. Perigynium, side view. F. Perigynium, front view. G. Perigynium, top view. H. Achene, front view. I. Achene, top view. J. Staminate scale. K. Anther. Bar equals 5 cm in A, 1 cm in B, 5 mm in C, and 0.5 mm in D–K. Drawn by Susan A. Reznicek from *Nee & Whalen 16809* (WIS).

shorter and more densely flowered lateral spikes 4–21 mm long, and a more compact inflorescence with the lowest two spikes 0.2–1.3 (–2.9) cm distant. *Carex virescens* has longer anthers ca 1.5–2.5 mm long, finely and inconspicuously red-dotted perigynia, strongly and uniformly pubescent leaves, longer lateral spikes (12–) 18–35 mm long that are often ± loosely flowered at the base, and a more open inflorescence with the lowest two spikes (1.2–) 1.8–3.5 (–5.8) cm distant. Plants of *C. tovarensis* are also ± stiffly erect and with the inflorescence stiff and straight. *Carex virescens* is a spreading plant with the inflorescence lax and flexuous or arcuate. The North American *Carex swanii* (Fernald) Mack. is similar to *C. virescens*, but smaller and with shorter anthers, spikes, and inflorescences. It, too, differs from *C. tovarensis* in having finely and inconspicuously red-dotted perigynia, strongly and uniformly pubescent leaves, and being a spreading plant with the inflorescence lax and flexuous or arcuate.

The only other member of *Carex* section *Porocystis* that occurs in South America is *C. boliviensis* Van Heurck & Müll-Arg. This species ranges from the Sierra de Córdoba in central Argentina to Peru, and also occurs in central Mexico (Hermann 1974); it grows primarily on grassy slopes and moist meadows at high elevations (up to 4100 m). *Carex tovarensis* differs from *C. boliviensis* in a number of features, the most salient of which are given in the key below.

Perigynia pilose, at least distally, strongly red-dotted; basal leaf sheaths reddish purple; rhizomes short. *C. tovarensis.*

Perigynia glabrous, not conspicuously red-dotted; basal leaf sheaths brownish; rhizomes elongate. *C. boliviensis.*

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TAXONOMIC STATUS, ECOLOGY, AND DISTRIBUTION OF CAREX HYALINA (CYPERACEAE)

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Carex hyalina Boott is a poorly understood species of the southeastern United States in the difficult and species-rich section *Ovales* Kunth. It was first described by Boott (1845) from a Drummond specimen collected along the Rio Brazos, Texas, but was later put by Boott (1862) into the synonymy of his broadly defined *C. straminea* Willd. Mackenzie (1931) resurrected *Carex hyalina* as a species and first distinguished it from the many other members of section *Ovales* within its range. Subsequently, essentially all authors have recognized it as a good species. Mackenzie reported *C. hyalina* only from Texas and Arkansas. The first report of the species from Oklahoma appears to be by Waterfall (1960). Finally, Orzell and Bridges (1987) summarized the distribution of the species up to that point, but *Carex hyalina* remained an obscure species with a poorly known distribution. Our aim is to remove this obscurity by clarifying the status of *C. hyalina*, including typifying the name, providing a comprehensive description, and distinguishing it from other species in the section. In addition, we provide information on its distinctive ecology as well as an up-to-date distribution map, supported by specimen citations, that considerably expands the known distribution of the species.

Carex hyalina Boott, Boston J. Nat. Hist. 5: 112. [7 Jan] 1845.—TYPE: Texas, [?Rio Brazos, 1833,] *Drummond s.n.* "from Mr Borrer & Mr Christy. 1836." (holotype: K!; probable isotypes: Texas. Rio Brazos, *Drummond s.n.*, 1833, BM!, K-4 sheets!).

Loosely colonial in small patches by short-creeping rhizomes, rhizomes 0.5–7 mm long between shoots; fertile culms 25–95 cm tall, trigonous, smooth except just below inflorescence, where finely scabrous-angled; bladeless basal sheaths pale brown, rapidly disintegrating into short, dark brown fibers. Leaves 4–7, on the lower 1/5–2/5 of the culm; blades ca. 3–20 cm long, 1–2.7 mm wide, plicate, glabrous, the margins antrorsely scabrous; leaf sheaths ca. 2–8 cm long, tightly enveloping culms, glabrous, green; the inner band of sheaths glabrous, whitish hyaline, prolonged ca. 0.4–1.6 mm beyond the ± auriculate leaf bases, the apex concave, whitish; ligules 2–3.5 mm long, rounded, the free portion entire to ± erose, up to 0.7 mm long. Vegetative culms very different from the fertile, fully developed only after the perigynia are largely shed, annual or occasionally overwintering, but never becoming fertile, 12–40 cm tall with ca. 10–35 leaves; leaves tristichous and mostly clustered in the upper 1/4 of the culm, often larger than

those of the fertile culms, ca. 4–25 cm long and up to 3 mm wide. Inflorescences 1.3–4 cm long, the upper spikes usually overlapping, the lowest two spikes 2–9 mm distant; spikes single at nodes, sessile, lowermost bracts scalelike or sometimes with a setaceous awn, 0.4–3.7 cm long, inconspicuous, sheathless, the upper bracts much reduced; spikes 2–4 (–6), gynaecandrous; terminal spikes often slightly larger than the lateral, but otherwise essentially similar, clavate-ovoid, 8–18 mm long, pistillate portion 6–12.5 mm long, 6.5–12 mm wide, ca. 5–25 (–30)-flowered, staminate portion 1–8 (–11) mm long, 0.7–1.2 mm wide, ca. 2–10-flowered. Pistillate scales 2.3–3.8 mm long, 0.8–1.6 mm wide, narrowly ovate, obtuse to acute, silvery white to pale brown with a narrow green center, 1-nerved. Staminate scales 2.4–4.5 (–5.2) mm long, 1.1–1.6 mm wide, lanceolate to narrowly ovate, acute to acuminate, silvery white to pale brown with a narrow green center, 1-nerved. Perigynia (4–) 4.5–6.6 mm long, 2.2–3.5 mm wide, 1.6–2.4 times as long as wide, widely spreading at maturity, plano-convex to ± biconvex with elliptic to ± suborbicular bodies (2.2–) 2.8–4.7 mm long, 0.9–1.6 times as long as wide, widest 1–2.4 mm above base (0.2–0.4 of the total perigynium length), broadly winged and serrulate-margined except near base, ± smooth or finely papillate, gradually tapered into a beak, green to pale brown, glabrous, sessile, adaxial side 3–7-nerved over achene, abaxial side 5–10-nerved over achene; beaks 1.4–2.8 mm long, 0.3–0.8 times as long as the body, strongly flattened and serrulate-margined to apex, the apex bidentate with scabrous-margined teeth ca. 0.1–0.4 mm long. Achenes 1.8–2.6 mm long, 0.9–1.2 mm wide, 1.7–2.4 times as long as wide, biconvex, narrowly ovate-oblong, pale brown, short-stipitate; style straight or very slightly contorted; stigmas 2. Anthers 3, ca. (1.1–) 1.3–2.6 mm long.

Specimens Examined. Arkansas. Hempstead Co.: near Fulton, 18 Apr 1901, *Canby 186 et al.* (GH); Fulton, 26 Apr 1905, *Bush 2459* (MO). Jackson Co.: near Newport, 26 Apr 1929, *Palmer 35530* (GH, MO); Hwy 69 at the Black River, west of Jacksonport, 27 Apr 1989, *Jones & Jones 2531* (MICH, TAES); Jacksonport, Jacksonport State Park, near the White River, 14 May 1989, *Naczi 2171* (MICH, UARK, ctb). Little River Co.: 2.7 mi SW of Foreman along S side of rte. 108, just E of French Bayou, SE 1/4 sec. 29 T12S R32W, 16 May 1988, *Naczi 1913* (MICH). Miller Co.: 27 Apr 1905, *Bush 2475* (GH, MO); Texarkana, 28 Apr 1905, *Bush 2500* (MO). Pulaski Co.: May 1886, *Hasse s.n.* (KANU). St. Francis Co.: Linden Island south end of Madison, 29 May 1960, *McDaniel 1872* (ctb).—Mississippi. Coahoma Co.: 2.5 mi NW of Lula, sect. 16, 2 May 1971, *McDaniel 15046* (ctb); 2.5 mi NW of Lula, N of hwy US 49, T7S R13W, sec. 12 or 13, 24 Apr 1992, *Bryson 11381 & Newton* (MICH, ctb). Tunica Co.: ca. 5 mi S of Tunica, 24 Apr 1992, *Bryson 11389 & Newton* (MICH, ctb); ca. 4 mi SE of Tunica, 24 Apr 1992, *Bryson 11396 & Newton* (MICH, ctb); ca. 11 mi S of Tunica, 24 Apr 1992, *Bryson 11408 & Newton* (MICH, ctb).—Oklahoma. McCurtain Co.: 7 mi S & 1 E of Idabel, 15 Apr 1950, *Waterfall 9325* (BRIT/SMU, OKLA); 7 mi S of Idabel, 18 Apr 1954, *Waterfall 11805* (OKLA, TEX); 3.6 mi S of jct. of RR and rte. 259 in Idabel, along W side of rte. 259, 14 May 1988, *Naczi 1882* (BRIT/SMU, DUR, MICH, ctb).—Texas. Bowie Co.: ca. 10 mi W of Bassett, 1.3 mi N of rte. 259–I-30 jct., along N side Sulphur River E of rte. 259, 11 May 1987, *Naczi 1567* (MICH). Brazoria Co.: Columbia, 31 Mar 1902, *Bush 1261* (GH, MO). Cass Co.: 4.4 mi NE of Naples, 11 May 1949, *Cory 55940* (BRIT/SMU). Dallas Co.: Dallas, Apr 1876, *Reverchon s.n.* (GH); Dallas, 1880, *Reverchon s.n.* (BRIT/SMU, NY); Dallas, 26 Mar 1901, *Reverchon s.n.* (GH, MO); Oak Cliff, 7 May 1901, *Reverchon 2426* (MO). Denton Co.: ca. 5 mi E of Denton: S of rte. 380 along W side of Trinity River, 10 May 1988, *Naczi 1859* (MICH, TAES, TEX). Houston Co.: along rte. 7, one mile east of Trinity River, 11 Apr 1964, *Correll & Correll 29125* (BRIT/SMU, LL). Lamar Co.: near Paris, Apr 1933, *Hampton s.n.* (US). Liberty Co.: Jct. of Hwy 162 and the Trinity River, SW side of the River, 4 May 1972, *Nixon 4637* (ASTC); 0.8 mi W on Hwy 105 from its jct. with the East Fork of the Trinity River, 8 May 1989, *Jones 2729 & Wipff* (ASTC, BRIT/SMU, MICH, TAES). Madison Co.: about 1 mi NW and W of the intersection of Hwy 21 and Trinity River, 7 Apr 1972, *Nixon 4063* (ASTC). Morris Co.: along E side of route 259 just W of the Sulphur River bridge (just N of I-30), 5 Jun 1989, *Reznicek 8489 & Naczi* (MICH, TAES, TRTE, WARM, ctb). Polk Co.: Trinity River, 8.7 mi S on Hwy 59 from its jct with Hwy 190 in Livingston, 11 May 1988, *Wipff 830 &*

FIGS. 1, 2. Perigynia and inflorescences of *Carex hyalina*. Fig. 1. Perigynia showing long beaks (from living plant vouchered by *Reznicek 8489 & Naczi*). Scale: bar = 1 mm. Fig. 2. Inflorescences showing perigynia spreading in the spikes (from living plant vouchered by *Reznicek 8489 & Naczi*). Scale: bar = 1 cm.

Jones (MICH, PAUH, SAT, jkw, sdj). Red River Co.: ca. 4 mi SE of Johntown: N of Sulphur River along W side rte. 271, 11 May 1988, *Naczi 1864* (MICH, TEX, UARK). Walker Co.: Trinity River bottom, 20 Apr 1938, *Warner 29* (CM, TEX); Sam Houston National Forest, Stubblefield Lake, SW of Huntsville, 11 Apr 1992, *Jones & Jones 8243* (MICH, TAES).—WITHOUT DEFINITE LOCALITY: Herb. Boott ex herb. Chapman (K).

Specimens considered isotypes vary in the completeness of their label data, but all appear to be part of the same gathering, and it seems reasonable that Drummond should have found this uncommon species only once. The origin of the Chapman specimen noted by Boott (1862) is somewhat of a mystery, as *Carex hyalina* apparently does not occur in the areas where Chapman did most of his collecting. The specimen, however, looks suspiciously similar to the Drummond collections in aspect, stage of maturity, and preparation, and perhaps Chapman obtained one of these and failed to record the data. All three collections cited for this species by Orzell and Bridges (1987) were seen, but not at NY or PH, the herbaria they cited.

The affinities of *Carex hyalina* are somewhat uncertain. In spite of being poorly understood, it is actually a quite distinctive species with no apparent close relatives. The key in Jones and Reznicek (1991) effectively separates it from all the Texas species of section *Ovales*. In fact, the combination of large perigynia [(4–) 4.5–6.6 mm long, 2.2–3.5 mm wide], 3–7-nerved adaxially over the achene with long (1.4–2.8 mm), somewhat poorly defined beaks (Fig. 1), and spreading perigynia in few-flowered [5–25 (–30)] spikes (Fig. 2) is unique among members of section *Ovales* in the southeastern United States. The distinctive habit, colonial by short-prolonged rhizomes producing numerous, well-developed vegetative culms, as well as the slender, few-spiked [2–4 (–6)] fertile culms allow *C. hyalina* to be readily recognized in the field. Correll and Johnson (1970) note that the species that most resembles *C. hyalina*, especially when immature, is *C. brittoniana* L. H. Bailey, a larger plant of open habitats distributed mostly to the west and south of the range of *C. hyalina*. *Carex brittoniana* shares with *C. hyalina* large, long-beaked perigynia spreading in relatively few, and sometimes few-flowered, spikes and may well be the closest relative of *C. hyalina*. However, *C. brittoniana* has longer and much wider perigynia [(5.5–) 6–8.3 mm long, 3.7–6 mm wide],

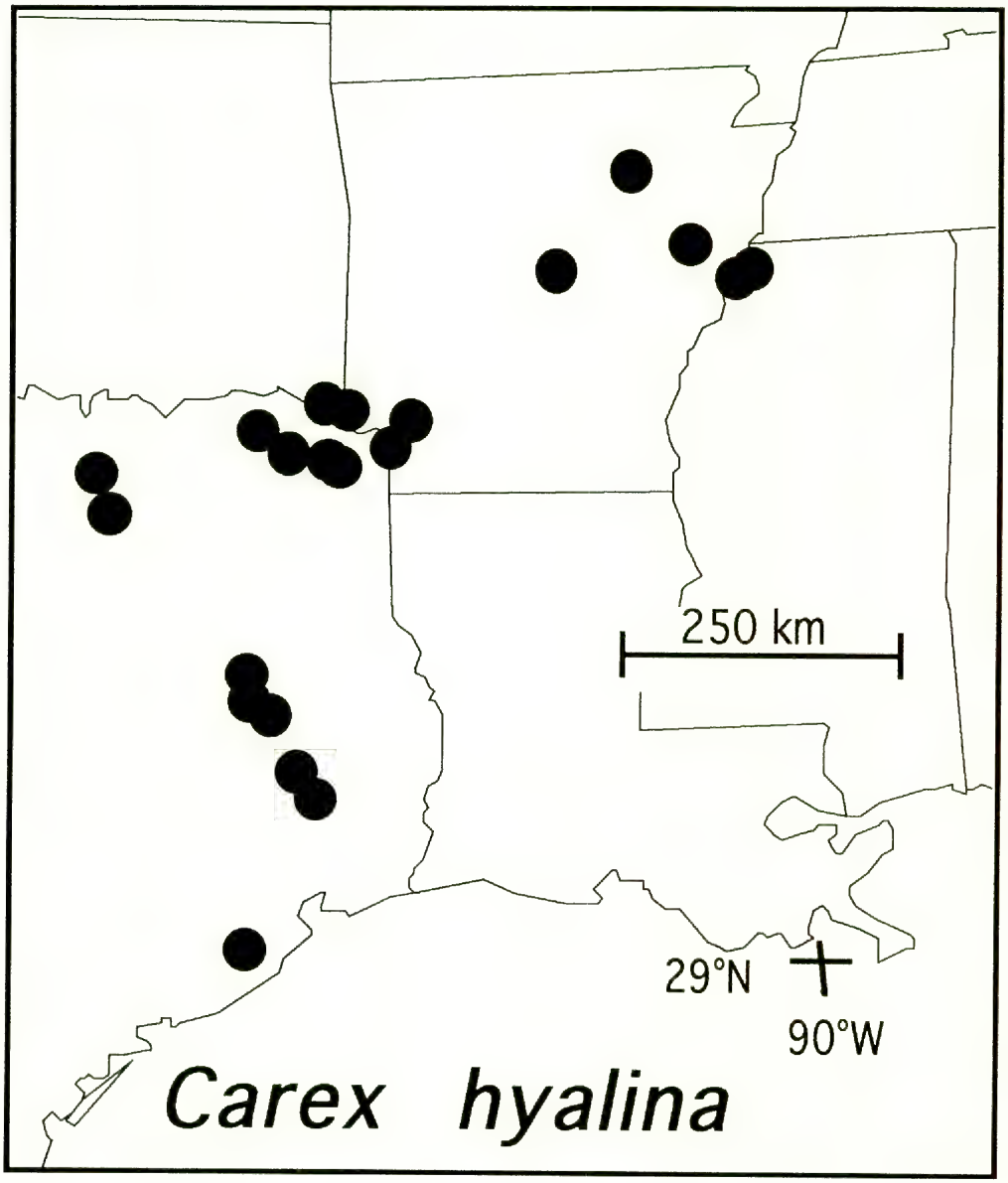

FIG. 3. Distribution of *Carex hyalina*.

which are nerveless adaxially over the achene. Very young specimens of *C. brittoniana*, without fully developed perigynia, can normally be separated from *C. hyalina* by their longer anthers [(2.1–) 2.6–4.4 mm long] and longer staminate scales (especially on the terminal spike, 4.8–8.1 mm long), which usually have the midrib excurrent as a distinct awn. *Carex brittoniana* also lacks the well-developed vegetative culms that are such a prominent feature of *C. hyalina*.

Boott (1862) and Mackenzie (1931) cite *Carex tetrastachya* Scheele (1849) as a later synonym of *C. hyalina*. Unfortunately, efforts to find the type ("prope Neubraunfels leg. Römer") have been fruitless. Scheele's herbarium appears to be lost, and few Römer specimens are known. New Braunfels, Texas (Comal County), is at the east edge of the Edwards Plateau, well west of the presently

TABLE 1. Results of analyses of soil samples from populations of *Carex hyalina*.

Locality	pH	Ca ppm	Fe ppm	K ppm	Mg ppm	P ppm	% org. matter	% sand	% silt	% clay	soil type
Arkansas: Little River Co., *Naczi 1913*	7.7	7897	5	295	191	17	4.0	29.8	22.0	48.2	clay
Mississippi: Coahoma Co., *Bryson 11381 & Newton*	7.0	4000	140	328	771	47	6.6	37.1	16.7	46.2	clay
Mississippi: Tunica Co., *Bryson 11389 & Newton*	5.3	4000	139	480	922	55	5.4	17.1	14.7	68.2	clay
Mississippi: Tunica Co., *Bryson 11396 & Newton*	5.4	3663	155	516	986	62	5.5	15.1	18.7	66.2	clay
Texas: Morris Co., *Reznicek 8489 & Naczi*	7.0	6960	53	298	303	27	4.9	61.8	12.0	26.2	sandy clay loam
Texas: Red River Co., *Naczi 1864*	7.5	8439	5	442	350	21	2.8	43.1	10.7	46.2	clay
MEAN VALUES	6.7	5827	83	393	587	38	4.9	34.0	15.8	50.2	clay

known range of *C. hyalina* (Fig. 3), which casts some doubt on Mackenzie's placement. The lack of information about the perigynia in the description may indicate that the Römer specimen was probably quite immature; however, Scheele described the scales of *C. tetrastachya* as "excurrente aristatae," which would apply to the staminate scales of *C. brittoniana*, a species known from the New Braunfels region, but not at all to *C. hyalina*. The Schlottmann specimen (Labady Prairies, Texas, K!) cited by Boott (1862) and sent to him by Sonder as an exemplar of Scheele's *C. tetrastachya* is a mixed collection of *C. brevior* (Dewey) Mack. and immature *C. brittoniana*. Mackenzie's other synonym, *C. straminea* "var. *hyalina* Boott," is not validly published, since Boott (1862) merely cited his *C. hyalina* as "a small variety" under his *C. straminea* var. *crawei*, and did not make the combination at varietal rank. Efforts to determine if this combination may have been made by later authors have thus far been unsuccessful.

Carex hyalina grows in shaded, wet soil of floodplains wooded with deciduous trees. Soils of *C. hyalina* habitats share several attributes (Table 1). The concentrations of calcium, potassium, magnesium, and phosphorous are high. In addition, the proportion of clay usually exceeds the silt and sand fractions. All but one of the soils analyzed possess a clay content greater than 45% and are classified as clays. The pH of these soils are usually nearly neutral. *Carex corrugata* Fernald is a constant or nearly constant associate of *C. hyalina* (Naczi & Bryson 1990). Other vascular plant species that frequently grow with *C. hyalina* include *C. blanda* Dewey, *C. bulbostylis* Mack., *C. cherokeensis* Schwein., *C. crus-corvi* Kunze, *C. socialis* Mohlenbr. & Schwegman, and *Ulmus crassifolia* Nutt.

Carex hyalina occurs in the west Gulf Coastal Plain and Mississippi Delta physiographic provinces in northwestern Mississippi, eastern and southwestern Arkansas, southeastern Oklahoma, and eastern Texas (Fig. 3). It grows in the drainage systems of a few large rivers: the Arkansas, Brazos, Mississippi, Red, St. Francis, Trinity, and White. Throughout its relatively small range, *C. hyalina* is often abundant where found, but local, probably due to its specific habitat. It should be sought on calcareous, alluvial clays elsewhere in the Southeast, especially in Louisiana, western Tennessee, and southeastern Missouri. The recent successes of field botanists in locating new populations of *C. hyalina* and expanding the known range of the species (Naczi & Bryson 1990; Bryson et al. 1992) emphasize how poorly known *C. hyalina* has been and make the discovery of the species in new regions quite likely. Only half a decade ago, *C. hyalina* was known from very few collections from a much smaller geographic range (Orzell & Bridges 1987). In fact, *C. hyalina* is currently being considered for addition to the United States List of Endangered and Threatened Plants (U.S. Fish & Wildlife Service 1990). Though *C. hyalina* is far from common, we believe its populations and individuals to be sufficiently numerous and secure that legal protection of the species under the U.S. Endangered Species Act is unwarranted.

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INFRAGENERIC NOMENCLATURE: CORRECTIONS AND ADDITIONS IN THE CARYOPHYLLACEAE

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INTRODUCTION

A major task facing the author of a family treatment for the *Generic Flora of the Southeastern United States* involves investigation of the infrageneric nomenclature of each genus known from the region. In the Caryophyllaceae, I discovered problems in the infrageneric nomenclature of nine genera. The intent of this paper is to report changes that are necessary to support the infrageneric classification I intend to present in the *Generic Flora* treatment.

Errors involving infrageneric nomenclature may be of several types. One of the most prevalent involves assumptions of rank for names that were published without a clear indication of rank. A primary example is the treatment of the Caryophyllaceae in Boissier's *Flora Orientalis* (1867). This work is often cited as the source for a number of section names in several of the large genera in the Caryophyllaceae (e.g., *Dianthus*, *Gypsophila*, and *Silene*). In each of these cases, the epithet appears in boldface preceded by "§"; in many works, this mark does indicate the rank of section (Stearn 1966). While Boissier used this mark for the single infrageneric divisions in *Dianthus* and *Minuartia*, he also used it within ranked infrageneric divisions in other genera. In *Cerastium* and *Gypsophila*, epithets preceded by § are used within sections (so designated). The 31 epithets preceded by § in *Silene* appear within series and subseries that Boissier does designate. I follow Chater and Walters (1964), Devjatov (1987), McNeill (1962), Reeve (1967), and Sourková (1977) in assuming such combinations, in various genera, to be unranked.

Another common error involves adoption of names that were proposed but not validly published. Volume 6 of the *Flora URSS* (Schischkin 1936) included a significant treatment of the Caryophyllaceae. In treating the larger genera (e.g., *Dianthus, Gypsophila*, and *Silene*), Schischkin included an infraspecific classification for each of them, often with many new names and combinations. All of his new taxa were described in Russian without accompanying Latin and thus are not validly published, since Article 36.1 of the Code requires a Latin description or diagnosis for any name published after 1 January 1935.

Two other errors that are sometimes seen involve the use of names that are not validly published, because they were given a rank contrary to the hierarchy established in Art. 5, e.g., Fenzl's use of "Divisio" within a section of *Cerastium* in Ledebour (1841–1843, *Cerastium*, p. 396–416, published in 1842 fide Stafleu & Cowan, 1979), and the incorrect typification of infrageneric names that are based on monotypic genera, e.g., Barkoudah's (1962) errors in *Gypsophila*.

A few changes are necessitated by changes in application of infrageneric autonyms. In three editions of the Code (Lanjouw et al. 1956, 1961, 1966), Art. 22 included the following statement: "a section including the type species of any subgenus must bear as its epithet the correct epithet of the subgenus." Wood and Webster (1968) proposed "to restrict the tautonymic provisions of Articles 19, 22, and 26 to taxa which include the nomenclatural types." These proposals were accepted at the 1969 Seattle Congress (Stafleu 1970) but led to subsequent debate (summarized in Brummitt, 1981) and extension of their concept to all infrageneric ranks at the Sydney Congress (Voss 1982). In the current edition of the Code (Greuter et al. 1988), Art. 22.1 and Note 1 continue to allow autonyms only for taxa including the type of the generic name; all other names must have a description or diagnosis or be associated with a reference to such (Art. 32.1). Article 34.3, allowing valid publication "where the same combination is simultaneously used at different ranks," allows many of the autonyms formed under pre-1969 provisions to stand unless an earlier name exists.

One assumption that I have made in this presentation deserves additional comment. In several pre-1953 cases, e.g., *Arenaria* sect. *Eremogone*, it is not entirely clear whether an author, by not adopting an earlier available epithet, is deliberately publishing a new name or actually making (although implicitly) a new combination. I have assumed the latter argument here, with the earliest name serving as the basionym even if it was not explicitly cited. Later variant spellings of homotypic names are then rejected under Art. 75 and heterotypic names under Art. 64.

The necessary changes in Caryophyllaceae are presented below, arranged alphabetically by genus. Only names that require changes are presented.

CORRECTIONS BY GENUS

Arenaria

McNeill (1962) revised most of the infrageneric nomenclature in *Arenaria*. He described series within five sections and used [then] autonyms for the series that included the type of the section; use below the section level was not mandated (nor prohibited) by the Code (Lanjouw et al. 1961) at that time.

One of the series, *Arenaria*, is now mandated under Art. 22.1. The other four were validly published, since McNeill provided a Latin description, type citation, and a clear indication of rank for each name. McNeill cited *Arenaria* sect. *Eremogone* as an "autonym" within *Arenaria* subg. *Eremogone*; the correct citation is given below.

Arenaria sect. **Eremogone** (Fenzl) Edgew. & Hook. f., Fl. Brit. India 1: 236. 1874 ["Eremogoneae"]. *Eremogone* Fenzl, Vers. Darst. Verbr. Alsin. 13. 1833. *Arenaria* a. *Eremogone* (Fenzl) Fenzl in Endl., Gen. pl. 967. 1840.—LECTOTYPE: *Arenaria graminifolia* Schrader (vide McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 121. 1962).

Cerastium

The citation for *Cerastium* sect. *Schizodon* must be changed to reflect an earlier combination. Although Williams cited the name as "Sect. *Schizondontia*,"

he did include *Cerastium dichotomum* L., one of the two syntypes included in Fenzl's protologue and here designated as the lectotype of the name of the section.

Cerastium sect. **Schizodon** (Fenzl) Williams, Bull. Herb. Boiss. 6: 899. 1898 ["Schizodontia"]. *Cerastium* b. *Schizodon* Fenzl. in Endl., Gen. pl. 970. 1840. *Cerastium* sect. *Schizodon* (Fenzl) Schischkin, Fl. URSS 6: 447. 1936.—LECTOTYPE, here designated: *Cerastium dichotomum* L.

Two of the subsectional names used by Rico (1990) require modification. The earliest name for the *C. fontanum* Baumg. complex is not *Cerastium* subsect. *Caespitosa* Pax & K. Hoffm. (1934) but the following (Art. 22.4.).

Cerastium subsect. **Vulgata** Hayek, Fl. Steierm. 1: 304. 1908.—TYPE: *Cerastium vulgatum* L., nom. ambig. [=*Cerastium fontanum* Baumg.].

The citation for *Cerastium* subsect. *Fugacia* must be changed. The authorship, given by Rico (1990) as Fenzl, is incorrect, since Fenzl treated the group as a "Divisio" in Ledebour (1841–1843, *Cerastium*, p. 396–416, published in 1842, fide Stafleu & Cowan, 1979); under Art. 33.4 the name is not validly published, since Fenzl's use of "Divisio" within a section is contrary to the hierarchy established in Art. 5. The correct citation is:

Cerastium subsect. **Fugacia** Hayek, Fl. Steierm. 1: 307. 1908.

DIANTHUS

1) *Ranking Boissier's names.* Rechinger (1988) assumed that § = section, in my opinion incorrectly, for five of the six sections that he recognized in his treatment of *Dianthus* in the *Flora Iranica*. Boissier (1867) noted that the species of *Dianthus* were closely related and "in sectiones naturales difficule distribuendae." Five names must be replaced by the earliest ranked combinations.

Dianthus sect. **Carthusiani** (Boiss.) F. Williams, J. Bot. 23: 341. 1885 ["Carthusianum"]. *Dianthus* § [without rank] 5. *Carthusiani* Boiss., Fl. Orient. 1: 481. 1867.

Dianthus sect. **Suffruticosi** F. Williams, J. Bot. 23: 341. 1885. *Dianthus* § [without rank] 4. *Dentati* Boiss., Fl. Orient 1: 480. 1867.

Dianthus sect. **Tetralepides** Pax in Engler, Nat. Pflanzenfam. 3(1b): 77. 1889. *Dianthus* § [without rank] 2. *Leiopetali* Boiss., Fl. Orient. 1: 479. 1867. *Dianthus* sect. *Tetralepides Leiopetala* F. Williams, J. Bot. 23: 346. 1885, nom. inval.

Dianthus sect. **Verruculosi** (Boiss.) Schischkin, Fl. URSS 6: 860. 1936. *Dianthus* § [without rank] 1. *Verruculosi* Boiss., Fl. Orient. 1: 479. 1867.

Dianthus sect. **Fimbriati** (Boiss.) F. Williams, J. Bot. 23: 343. 1885 ["Fimbriatum"]. *Dianthus* § [without rank] 3. *Fimbriati* Boiss., Fl. Orient. 1: 480. 1867.

2) *Usage of names proposed by Schischkin in 1936.* Schischkin included 14 new series names in his treatment of *Dianthus*. Validation of these names should await the desperately needed comprehensive revision of this genus.

3) *Sectional names that have priority.* Two sectional names must be replaced by earlier names.

Dianthus sect. **Armeriastrum** Ser. in DC., Prodr. 1: 355. 1824. *Dianthus* sect. *Armerium* F. Williams, J. Bot. 23: 340. 1885.—TYPE: *Dianthus armeria* L. (Art. 22.4).

Dianthus sect. **Chamaegarophalon** Griseb., Spic. Fl. Rumel. 1: 193. 1843. *Dianthus* sect. *Barbulatum* F. Williams, J. Bot. 23: 344. 1885.—LECTOTYPE, here designated: *Dianthus myrtinervius* Griseb.

GYPSOPHILA

Several nomenclature problems, mostly arising from Barkoudah's (1962) revision of *Gypsophila,* must be addressed.

1) *Ranking Boissier's names.* Barkoudah (1962) assumed, in my opinion incorrectly, that the six names set in boldface and preceded by § that Boissier (1867) included within sections should be considered as subsections. The authorship must therefore be changed in four of Barkoudah's subsectional combinations.

Gypsophila subsect. **Pulvinares** (Boiss.) Barkoudah, Wentia 9: 37. 1962. *Gypsophila* § [without rank] 1. *Pulvinares* Boiss., Fl. Orient. 1: 534. 1867.

Gypsophila subsect. **Caespitosae** (Boiss.) F. Williams, J. Bot. 27: 325. 1889. *Gypsophila* § [without rank] 3. *Cespitosae* Boiss., Fl. Orient. 1: 535. 1867.

Gypsophila subsect. **Paniculatae** (Boiss.) F. Williams, J. Bot. 27: 325. 1889. *Gypsophila* § [without rank] 4. *Paniculatae* Boiss., Fl. Orient. 1: 535. 1867.

Gypsophila subsect. **Suffruticosae** (Boiss.) Barkoudah, Wentia 9: 42. 1962. *Gypsophila* § [without rank] 5. *Suffruticosae* Boiss., Fl. Orient. 1: 535. 1867.

2) *Usage of names proposed by Schischkin in 1936.* As noted above, new names appearing in Schischkin (1936) are not validly published. Three names used, but not validated, by Barkoudah (1962) are validated here.

Gypsophila subsect. **Acutifoliae** Rabeler, subsect. nov. *Gypsophila* ser. "Acutifoliae" Schischkin, Fl. URSS 6: 757. 1936.—TYPE: *Gypsophila acutifolia* Fisch.

Plantae plus minusve glaucae, inflorescentia furcis valde glanduloso-pubescentibus instructa; calyx 3–4 mm longus, glaber, dentibus acutis.

Gypsophila ser. **Elegantes** Schischkin ex Rabeler, ser. nov. *Gypsophila* ser. "Elegantes" Schischkin, Fl. URSS 6: 763. 1936.—TYPE: *Gypsophila elegans* M. Bieb.

Herbae annuae vel rarius perennes; caules ramosi glabri. Petala alba vel rosea, emarginata, sepalis 2–4plo longiora, ovarium 12–18 ovulis instructum.

Gypsophila ser. **Hispidae** (Rech.f.) Schischkin ex Rabeler, stat. nov. *Gypsophila* ser. "Hispidae" Schischkin, Fl. URSS 6: 770. 1936. *Gypsophila* sect. *Hispidae* Rech.f., Fl. Iran 163: 241. 1988.—TYPE: *Gypsophila fedtschenkoana* Schischkin (Rechinger 1988).

Barkoudah's (1962) choice of *Gypsophila pilosa* Huds. as the type of this series has no standing, since the name for Schischkin's series was not validly published.

3) *Citation and typification of names involving monotypic genera.* When *Heterochroa* Bunge was described in 1830, Bunge included one species, *H. petraea* Bunge. Most subsequent authors have treated Bunge's genus as *Gypsophila* sect. *Heterochroa* (Bunge) Fenzl (e.g., Barkoudah 1962; Rechinger 1988), based on Fenzl's treatment of the Caryophyllaceae in Endlicher's *Genera Plantarum* (1836–1840; *Gypsophila*, p. 971–972, published in 1840, fide Stafleu & Cowan, 1976). If one accepts the arguments of Brizicky (1969) for considering infrageneric names appearing in that volume "as published without an indication of rank,"as I did earlier in the case of *Petrorhagia* (Rabeler 1984), then Fenzl's combination is rankless and cannot be used. This is also consistent with McNeill's (1962) treatment of Fenzl's names in *Arenaria* and *Minuartia*. The corrected citation is:

Gypsophila sect. **Heterochroa** (Bunge) A. Braun, Flora 26: 383. 1843. *Heterochroa* Bunge in Ledebour, Fl. Alt. 2: 131. 1830. *Gypsophila* b. *Heterochroa* (Bunge) Fenzl in Endl., Gen. pl. 972. 1840.—TYPE: *Heterochroa petraea* Bunge [=*Gypsophila sericea* (Ser.) Krylov].

The choice of *Gypsophila microphylla* (Schrenk) Fenzl as the type of *Gypsophila* sect. *Heterochroa* by Barkoudah (1962) and Rechinger (1988) is incorrect. Bunge included a single species in his protologue of *Heterochroa*; according to Art. 10.2, the type of its name must be the type of the generic name. This type is maintained for all combinations involving that name (Art. 7.12).

The attribution of *Gypsophila* sect. *Dichoglottis* presents a similar situation. In 1835, Fischer and Meyer described *Dichoglottis*, including one species, *D. linearifolia* Fischer & C. Meyer. Most subsequent authors have included *Dichoglottis* within *Gypsophila*, most recently as a section (e.g., Barkoudah 1962; Rechinger 1988). In this case, Barkoudah (1962) attributed the combination to Boissier and did not recognize Fenzl's earlier subgeneric placement in Endlicher (1836–1840). Because an earlier combination exists, the correct citation is as follows.

Gypsophila sect. **Dichoglottis** (Fischer & C. Meyer) A. Braun, Flora 26: 383. 1843. *Dichoglottis* Fischer & C. Meyer, Index Sem. Hort. Petropol. 1: 25. 1835.—TYPE: *Dichoglottis linearifolia* Fischer & C. Meyer [=*Gypsophila linearifolia* (Fischer & C. Meyer) Boiss.].

The choice of *Gypsophila elegans* M. Bieb. as type of *Gypsophila* sect. *Dichoglottis* by Barkoudah (1962) and Rechinger (1988) is incorrect. Since Fischer and Meyer included a single species within *Dichoglottis*, the type of its name must be

the type of the name of the genus (Art. 10.2) and any subsequent combinations (Art. 7.12).

Within *Gypsophila* sect. *Dichoglottis*, Barkoudah (1962) described subsect. *Purpurae*, typifying it with *G. elegans* M. Bieb. Barkoudah (1962) included *G. capillaris* (Forssk.) C. Christ in *Gypsophila* subsect. *Purpurae*. *Rokejeka capillaris* Forssk. is the type of the monotypic genus *Rokejeka* Forssk. and an earlier subsectional combination in *Gypsophila*. Hence, Barkoudah's name and type fall into synonymy of the correct name:

Gypsophila subsect. **Rokejeka** (Forssk.) F. Williams, J. Bot. 27: 325. 1889 ["Rokejekae"]. *Rokejeka* Forssk., Fl. Aegypt. Arab. 90. 1775. *Gypsophila* subsect. *Purpurae* Barkoudah, Wentia 9: 44. 1962.—TYPE: *Rokejeka capillaris* Forssk. [=*Gypsophila capillaris* (Forssk.) C. Christ.].

4) *The correct name for Gypsophila subg. Pseudosaponaria.* Barkoudah (1962) followed Williams (1889) in recognizing *Gypsophila* subg. *Pseudosaponaria* Williams, but Rechinger (1988) accepted the name *Gypsophila* subg. *Hagenia* (Moench) Fenzl. Although *Gypsophila* sect. *Hagenia* is the correct name at the rank of section, *Hagenia* was not transferred to subgeneric rank until 1934. Contrary to Rechinger (1988), Fenzl (in Endlicher 1836–1840) did not make any combination involving *Hagenia* but included *Hagenia* in the synonymy of his "a. *Dichoglottis*."

LYCHNIS

Modifying Pax and Hoffmann's (1934) treatment of *Lychnis* to reflect more current views (Chater 1964; Jalas & Suominen 1986) requires adopting an autonym (*Lychnis* subg. *Lychnis* = Pax and Hoffmann's *Lychnis* subg. *Eulychnis* DC., nom. inval.) as well as one change in authorship and one new combination.

The correct author citation of *Lychnis* subgenus *Coronaria* is (Guett.) Pax, rather than (L.) Pax. Linnaean usage of *Coronaria* dates from 1737 (Gorshkova in Schischkin 1936), but Guettard was the first to adopt it after 1753 (Dandy 1967). Although two earlier combinations at this rank exist in Reichenbach (1828), neither can be used. Usage of *Lychnis* subg. *Agrostemma* (L.) Reichenb. would be counter to Art. 10.2 since the type of the generic name *Agrostemma* L. (*A. githago* L.) is excluded. Reichenbach also listed *Lychnis* subg. "Muscipula" Riv., a pre-Linnaean name that can be attributed to Ruppius (Pfeiffer 1874), as equivalent to *Coronaria* L.; the lack of a description (or correct reference to one) prevents usage (Art. 32).

The inclusion of the rather aberrant *Polyschemone nivalis* (Kit. ex J. A. Schultes) Schott, Nyman & Kotschy within *Lychnis* by Chater (1964) and Jalas and Suominen (1986) suggests the need for the following combination to emphasize the disparity between this species and other members of the genus.

Lychnis subg. **Polyschemone** (Schott, Nyman & Kotschy) Rabeler, comb. nov. *Polyschemone* Schott, Nyman & Kotschy, Analecta Bot. 55. 1854.—TYPE: *Lychnis nivalis* Kit. ex J. A. Schultes.

Minuartia

McNeill (1962), in revising the infrageneric classification of *Minuartia*, included seven autonyms at the series level. One of these, *Minuartia* ser. *Minuartia*, is expected. Names that Mattfeld published as series have priority over the remaining six; only one was used by both Mattfeld and McNeill. McNeill (1962) cited *Minuartia* subsect. *Spectabiles* (Fenzl) McNeill as an autonym; this combination is validly published under Art. 34.3.

Minuartia ser. **Biflorae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 183. 1922. *Minuartia* ser. *Spectabiles* McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 140. 1962.

Minuartia ser. **Laricifoliae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 182. 1922; McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 142. 1962.

Minuartia ser. **Cerastiifoliae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 136. 1922. *Minuartia* ser. *Lanceolatae* McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 143. 1962.

Minuartia ser. **Flaccidae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 148. 1922. *Minuartia* ser. *Acutiflorae* McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 145. 1962.

Minuartia ser. **Fasciculatae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 54. 1922. *Minuartia* ser. *Xeralsine* McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 149. 1962.

Minuartia ser. **Tenuifoliae** Mattf., Repert. Spec. Nov. Regni Veg. Beih. 15: 32. 1922. *Minuartia* ser. *Sabulina* McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 150. 1962.

Two of the sectional names used by McNeill (1962) require author citation changes to reflect earlier combinations made by Hayek (1908–1911; p. 273–277 published in 1908, fide Stafleu & Cowan, 1979).

Minuartia sect. **Aretioideae** (Fenzl) Hayek, Fl. Steierm. 1: 277. 1908.

Minuartia sect. **Sabulina** (Reichenb.) Hayek, Fl. Steierm. 1: 273. 1908 ["Sabulineae"].

The attribution of *Minuartia* subg. *Rhodalsine* must also be changed. McNeill (1962), citing *Minuartia* subg. *Rhodalsine* (Gay) Graebner, referred to p. 774 in Ascherson & Graebner (1913–1919; p. 774, published in 1918, fide Stafleu & Cowan, 1976) as the place of publication for this combination. Graebner indeed recognized this subgenus, but as *Minuartia* subg. *Psammophilae* (Fenzl) Graebner, and cited *Rhodalsine* in synonymy; under Art. 34.1(c), the combination McNeill cited is not validly published. Pax's earlier (1889) recognition of *Alsine*

subg. *Rhodalsine* (Gay) Pax, however, predates Graebner's combination, and allows retention of the name that McNeill chose. The correct citation is:

Minuartia subg. **Rhodalsine** (Gay) McNeill, Notes Roy. Bot. Gard. Edinburgh 24: 134. 1962.

Paronychia

Two of the subgeneric combinations proposed by Chaudhri (1968) had been previously published.

Paronychia subg. **Siphonychia** (Torrey & A. Gray) Reichenb., Deut. Bot.-Herb. Buch. 162. 1841; Chaudhri, Meded. Bot. Mus. Herb. Rijks. Univ. Utrecht 285: 82. 1968.

Paronychia subg. **Anoplonychia** (Fenzl) Reichenb., Deut. Bot.-Herb. Buch. 162. 1841; Chaudhri, Meded. Bot. Mus. Herb. Rijks. Univ. Utrecht 285: 91. 1968.

One of the three autonyms that Chaudhri (1968) chose within *Paronychia* subg. *Anoplonychia* (Fenzl) Reichenb. must be replaced by an earlier name.

Paronychia sect. **Anoplonychia** (Fenzl) Fenzl in Ledeb., Fl. Ross. 2: 162. 1843. *Paronychia* a. *Anoplonychia* Fenzl in Endl., Gen. pl. 958. 1839.

The other two names, *Paronychia* subsect. *Anoplonychia* (Fenzl) Chaudhri and *Paronychia* subsect. *Heterosepalae* (Chaudhri) Chaudhri, are validly published according to Art. 34.3; these names were simultaneously used for sections and subsections.

Saponaria

1) *Typification and placement of Spanizium.* Grisebach described the genus *Spanizium* in 1843, including a single species originally described in *Saponaria*, *Saponaria ocymoides* (L.) Griseb. Two separate issues arise from Grisebach's action: the identity of the type of the generic name and the placement of *Spanizium* when its type is included in *Saponaria*.

Shultz resurrected *Spanizium* in 1984, using it to segregate *Saponaria prostrata* Willd. from *Saponaria*. He argued (Shultz 1984, 1989) that Grisebach (1843) misidentified a specimen of *S. prostrata* as *S. ocymoides* when he described *Spanizium*. Shultz cited the type of *Spanizium* as "*S. ocymoides* (L.) Griseb. p.p. excl. basionymo (=*S. prostratum* (Willd.) V. A. Shultz)," an attempt to correct Grisebach's error. Article 10.2 does not allow such a correction; *Spanizium* must be typified by *S. ocymoides* regardless of what Grisebach either had in hand or should have written. Because Shultz explicitly excluded Grisebach's type of *Spanizium*, he created a later homonym of *Spanizium* (Art. 48). Two courses of action are possible. *Spanizium* sensu Shultz can be retained only if conserved with *S. prostratum* as the type (Art. 14.8). The alternative is a substitute name to segregate

Saponaria prostrata and *S. kotschyi* Boiss. from the rest of the genus. I refrain from either course, since I am not convinced of the validity of this segregation.

Boissier (1867) first used *Spanizium* as an infrageneric epithet within *Saponaria*, in this case with rank clearly indicated. He described *Saponaria* sect. *Spanizium* (Griseb.) Boiss., including two species, *S. kotschyi* and *S. prostrata*. A new name is required, since the type of *Spanizium*, *S. ocymoides*, is now placed in a different subgenus (Simmler 1910). According to Art. 10.2, the type of *Spanizium* must be *S. ocymoides* since Grisebach named only one species (*S. ocymoides*) in the protologue. The following name is thus proposed:

Saponaria sect. **Prostratae** Rabeler, nom. nov. *Saponaria* sect. *Spanizium* (Griseb.) Boiss., Fl. Orient 1: 529. 1867, descr. excl. type.—TYPE: *Saponaria prostrata* Willd.

2) *An overlooked subgeneric name.* Brizicky (1969) noted that one source of subgeneric names often overlooked is Reichenbach's *Conspectus regni vegetabilis*. The name *Saponaria* subg. *Saporhizaea* Simmler (1910) must be replaced by one such overlooked combination.

Saponaria subg. **Proteinia** (Ser.) Reichenb. Consp. Regn. Veg. 206. 1828 ["Proteina"]. *Saponaria* sect. *Proteinia* Ser. in DC., Prodr. 1: 366. 1824. *Saponaria* subg. *Saporhizaea* Simmler, Denkschr. Kaiserl. Acad. Wiss., Math.-Naturwiss. Kl. 85: 456. 1910.—LECTOTYPE: *Saponaria orientalis* L. (vide Shultz, Bot. Zhurn. 69: 1479. 1984).

SILENE

Chowdhuri (1957) published the most recent synopsis of *Silene*, in which he divided the genus into 44 sections including 44 subsections. A number of problems exist in his nomenclature.

1) *Ranking Boissier's names.* As discussed above, I suggest that names set in boldface and preceded by § in Boissier's *Flora Orientalis* (1867) be treated as unranked combinations. In his remarks about *Silene* (p. 567), Boissier admitted the genus is not well understood, stated clearly "non sectiones proposui," and placed "species Orientales in greges quoad potuerim naturales"; these greges are the 31 groups with names preceded by § and assumed by Chowdhuri (1957) to be sections. The citations of the following 14 names have been modified to reflect the first clear ranking as sections. Some of these combinations appear in Chater and Walters (1964); yet, the fact that Melzheimer (1988) followed Chowdhuri (1957) in his recent *Silene* treatment in *Flora Iranica* suggests the desirability to present them here.

Silene sect. **Italicae** (Rohrb.) Schischkin, Fl. URSS 6: 675. 1936. *Silene* § [without rank] 19. *Paniculatae* Boiss., Fl. Orient. 1: 574. 1867. *Silene* ser. *Italicae* Rohrb. Monogr. Silene 77. 1868.

Silene sect. **Lasiostemones** (Boiss.) Schischkin, Fl. URSS 6: 631. 1936. *Silene* § [without rank] 21. *Lasiostemones* Boiss., Fl. Orient. 1: 574. 1867.

Silene sect. **Sclerocalycinae** (Boiss.) Schischkin, Fl. URSS 6: 636. 1936. *Silene* § [without rank] 23. *Sclerocalycinae* Boiss., Fl. Orient. 1: 575. 1867.

Silene sect. **Tunicoideae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957. *Silene* § [without rank] 30. *Tunicoideae* Boiss., Fl. Orient. 1: 577. 1867.

Silene sect. **Spergulifoliae** (Boiss.) Schischkin, Fl. URSS 6: 652. 1936. *Silene* § [without rank] 14. *Spergulifoliae* Boiss., Fl. Orient. 1: 572. 1867.

Silene sect. **Ampullatae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957. *Silene* § [without rank] 12. *Ampullatae* Boiss., Fl. Orient. 1: 571. 1867.

Silene sect. **Fimbriatae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957. *Silene* § [without rank] 17. *Fimbriatae* Boiss., Fl. Orient. 1: 574. 1867.

Silene sect. **Brachypodae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957. *Silene* § [without rank] 24. *Brachypodae* Boiss., Fl. Orient. 1: 575. 1867.

Silene sect. **Auriculatae** (Boiss.) Schischkin, Fl. URSS 6: 656. 1936. *Silene* § [without rank] 15. *Auriculatae* Boiss., Fl. Orient. 1: 572. 1867.

Silene sect. **Compactae** (Boiss.) Schischkin, Fl. URSS 6: 615. 1936. *Silene* § [without rank] 6. *Compactae* Boiss., Fl. Orient. 1: 569. 1867.

Silene sect. **Succulentae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957. *Silene* § [without rank] 25. *Succulentae* Boiss, Fl. Orient. 1: 576. 1867.

Silene sect. **Saponarioideae** (Boiss.) Schischkin, Fl. URSS 6: 682. 1936. *Silene* § [without rank] 3. *Saponarioideae* Boiss., Fl. Orient. 1: 568. 1867.

Silene sect. **Rigidulae** (Boiss.) Schischkin, Fl. URSS 6: 681. 1936. *Silene* § [without rank] 11. *Rigidulae* Boiss., Fl. Orient. 1: 571. 1867.

Silene sect. **Lasiocalycinae** (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957. *Silene* § [without rank] 8. *Lasiocalycinae* Boiss., Fl. Orient. 1: 569. 1867.

Melzheimer's (1988) attributions of the following two sectional names are likewise corrected here.

Silene sect. **Scorpioideae** Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957. *Silene* § [without rank] 9. *Bipartitae* Boiss., Fl. Orient 1: 594. 1867. *Silene* ser. *Bipartitae* (Boiss.) Rohrb., Ann. Sci. Nat. Bot. V. 8: 371. 1868. *Silene* ser. *Scorpioideae* Rohrb. Monogr. Silene 67. 1869, nom. superfl.

Silene ser. *Bipartitae* appears in Rohrbach's *Conspectus* (1868), replaced without explanation with *Silene* ser. *Scorpioideae* in his later *Monographie* (1869). Although derived from the superfluous series name, *Silene* sect. *Scorpioideae* Chowdhuri is the correct name under Art. 60 and Art. 72, Note 1.

Silene sect. **Schaftae** (Boiss.) Melzheimer, Fl. Iran 163: 466. 1988. *Silene* § [without rank] 29. *Schaftae* Boiss., Fl. Orient. 1: 577. 1867.

2) *Usage of names proposed by Schischkin in 1936.* Chowdhuri (1957) adopted three of the sections and 13 of the series names that first appeared in Schischkin's treatment of *Silene* in *Flora URSS* (Schischkin 1936). Although he assumed Schischkin published the series names as subsections, he did realize that none were validly published and provided each with a Latin description and typification. Unless preempted by an earlier combination (noted below), names that Chowdhuri (1957) based on Schischkin's names are validly published and to be ascribed solely to him.

3) *Overlooked subsectional combinations.* Names of twelve of the new subsections that Chowdhuri (1957) described as well as one combination that he made must be changed, because the subsectional combinations based on Rohrbach's (1869) series names were already proposed by Gürke (in Richter 1897–1903, fasc. 2, p. 161–320, published in 1899, fide Stafleu & Cowan, 1983). In all but one case, these changes are in the spirit of Recommendation 22A of the Code; the name of a subsection including the type of the sectional name repeats the sectional epithet.

Silene subsect. **Italicae** (Rohrb.) Gürke in Richter, Pl. Eur. 2: 317. 1899. *Silene* subsect. *Patulae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957.

Silene subsect. **Sclerocalycinae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 310. 1899. *Silene* subsect. *Longiflorae* Schischkin ex Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957.

Silene subsect. **Chloranthae** (Rohrb.) Gürke in Richter, Pl. Eur. 2: 310. 1899. *Silene* subsect. *Ecoranatae* Schischkin ex Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957.

Silene subsect. **Spergulifoliae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 314. 1899. *Silene* subsect. *Polyphyllae* Schischkin ex Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957.

Silene subsect. **Suffruticosae** (Rohrb.) Gürke in Richter, Pl. Eur. 2: 311. 1899. *Silene* subsect. *Aucherianae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 239. 1957.

Silene subsect. **Brachypodae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 303. 1899. *Silene* subsect. *Nutantes* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957, non *Silene* subsect. *Nutantes* (Rohrb.) Gürke, 1899.

Silene subsect. **Auriculatae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 298. 1899. *Silene* subsect. *Brevicaules* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957.

Silene subsect. **Macranthae** (Rohrb.) Gürke in Richter, Pl. Eur. 2: 299. 1899. *Silene* subsect. *Saxifragae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957.

Silene subsect. **Atocion** (Otth) Gürke in Richter, Pl. Eur. 2: 304. 1899. *Silene* subsect. *Delicatulae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957.

Silene subsect. **Leiocalycinae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 307. 1899. *Silene* subsect. *Muscipulae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957.

Silene subsect. **Lasiocalycinae** (Boiss.) Gürke in Richter, Pl. Eur. 2: 309. 1899. *Silene* subsect. *Squamatae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957.

Silene subsect. **Eudianthe** (Reichenb.) Gürke in Richter, Pl. Eur. 2: 309. 1899. *Silene* subsect. *Eudianthe* (Reichenb.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957.

Silene subsect. **Scorpioideae** (Rohrb.) Gürke in Richter, Pl. Eur. 2: 291. 1899. *Silene* subsect. *Pubicalycinae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957.

4) *Silene sect. Melandriformes Chowdhuri – a mixed concept.* As Chater and Walters (1964) correctly noted, there is an earlier name for Chowdhuri's (1957) *Silene* sect. *Melandriformes* (Boiss.) Chowdhuri. The type of *Silene* sect. *Melandriformes*, based on one of Boissier's unranked names, is *S. noctiflora* L., one of two species (the other is *S. elisabethae* Jan) that Fenzl included in his description of *Saponaria* γ *Elisanthe* (in Endlicher 1836–1840, *Saponaria*, p. 972, published in 1840 fide Stafleu & Cowan, 1976). The presence of a calyx inflated only in fruit in *S. noctiflora* rather than, as in *S. eliabethae*, both at anthesis and in fruit, places *S. noctiflora* in agreement with Fenzl's description; it is here designated as the lectotype of Fenzl's unranked group and therefore of the following sectional combination:

Silene sect. **Elisanthe** (Fenzl) Ledeb., Fl. Ross. 1: 314. 1842.—LECTOTYPE: *Silene noctiflora* L.

Chowdhuri (1957) considered it best to merge *Melandrium* Röhl. with *Silene* and transferred the so-called "true" melandriums (*Melandrium* sect. *Melandrium*, e.g., *Silene latifolia* Poir.) into *Silene* sect. *Melandriformes*. As noted above, this sectional name is typified by *S. noctiflora*, a species that, although also often included in *Melandrium*, has always been separated from members of sect. *Melandrium*. Both Ledebour (1841–1843, ordo *Sileneae*, p. 273–337, published in 1842, fide

Stafleu & Cowan, 1979) and Boissier (1867) recognized *Melandrium* but placed *S. noctiflora* in *Silene*. Pax (1889) and later Pax and Hoffmann (1934) included *S. noctiflora* in *Melandrium* as a member of *Melandrium* sect. *Elisanthe* (Fenzl) A. Braun.

In their study of the chloroplast DNA in European members of *Silene* sect. *Elisanthe*, Sandbrink et al. (1989) repeatedly emphasized that *S. noctiflora* was quite isolated, confirming what previous morphological and breeding studies had indicated. They "suggest[ed] that *S. noctiflora* is not correctly classified in *Silene* section *Elisanthe*." Since *S. noctiflora* is the lectotype of sect. *Elisanthe*, the conclusion must be reversed; the other members should be removed from sect. *Elisanthe*. To accomplish the traditional segregation of these taxa within *Silene*, I propose the following new combination:

Silene sect. **Melandrium** (Röhl.) Rabeler, comb. nov. *Melandrium* Röhl., Deutsch. Fl. ed. 2. 2: 37, 274. 1812. *Melandrium* sect. *Melandrium* in A. Braun, Flora 26: 371. 1843 ["Eumelandrium"].—TYPE: *Melandrium silvestre* (Schkuhr) Röhl. [=*Silene dioica* (L.) Clairv.].

5) *Miscellaneous corrections.* The citation for *Silene* sect. *Chloranthae* must be changed. Chowdhuri (1957) cited Rohrbach as the author of the sectional name, but Rohrbach (1868, 1869) used it for a series in *Silene*, not a section. The correct citation should be:

Silene sect. **Chloranthae** (Rohrb.) Schischkin, Fl. URSS 6: 616. 1936.

As Bocquet (1967) noted, Chowdhuri's (1957) *Silene* sect. *Gastrolychnis* (Fenzl) Chowdhuri must be replaced by the earlier name *Silene* sect. *Physolychnis* (Bentham) Bocquet. Operating under the Art. 22 provisions in effect at that time, Bocquet used an autonym for the subsection including the type of *Silene* sect. *Physolychnis*. Since he provided rank, a Latin description, and typification for this name, it is validly published.

Silene subsect. **Physolychnis** (Bentham) Bocquet, Candollea 22: 6. 1967.

Silene sect. *Suffruticosae* (Rohrb.) Chowdhuri is predated by Schischkin's earlier publication of the combination. The corrected citation is:

Silene sect. **Suffruticosae** (Rohrb.) Schischkin, Fl. URSS 6: 646. 1936.

Silene sect. *Inflatae* (Boiss.) Chowdhuri must also be replaced by an earlier name. The lectotype that Chowdhuri (1957) selected, *Silene cucubalus* Wibel [=*S. vulgaris* (Moench) Garcke], is also the type of the monotypic genus *Behen* Moench and, under Art. 10.2, the type of the following combination.

Silene sect. **Behen** (Moench) Griseb., Spic. Fl. Rumel. 1: 170. 1843. *Behen* Moench, Meth. 709. 1794, non *Behen* Hill, 1762. *Silene* § [without rank] 16. *Inflatae* Boiss., Fl. Orient. 1: 573. 1867. *Silene* sect. *Inflatae* (Boiss.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957.—TYPE: *Behen vulgaris* Moench [=*Silene vulgaris* (Moench) Garcke].

The authorship of *Silene* sect. *Heliosperma* cited by Chowdhuri (1957) must be modified, because the combination in Reichenbach's *Flora germanica excursiora* is best treated as unranked (Brizicky 1969).

Silene sect. **Heliosperma** (Reichenb.) Ledeb., Fl. Ross. 1: 317. 1842. *Silene* "sect." *Heliosperma* Reichenb., Fl. Germ. Exc. 87. 1832.

When Talavera (1979) revised *Silene* sect. *Erectorefractae* Chowdhuri, he described two subsections for the seven included species. *Silene* subsect. *Erectorefractae* is presented as an autonym, contrary to Art. 22.1; however, since a clear citation of rank, typification, and a Latin description is included, the name is valid and the correct citation is:

Silene subsect. **Erectorefractae** (Chowdhuri) Talavera, Lagascalia 8: 145. 1979. *Silene* sect. *Erectorefractae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957.

Zuev (1990) examined Siberian taxa of *Silene* sect. *Graminifoliae* Chowdhuri and described two series for the four included species. *Silene* ser. *Graminifoliae* was presented as an autonym, contrary to Art. 22.1, with a clearly stated rank, a type designation, but with only a Russian description. The correct citation should be:

Silene ser. **Graminifoliae** Schischkin ex Rabeler, ser. nov. *Silene* ser. "Graminifoliae" Schischkin, Fl. URSS 6: 625. 1936. *Silene* sect. *Graminifoliae* Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 236. 1957.—TYPE: *Silene graminifolia* Otth.
Calyx nervis distinctis; caules (2–) 3–9 internodis instructi.

Silene sect. *Balcanosilene* Sourková (1977) must be replaced by the following earlier name that Panov (1974) proposed to segregate the same group of species from the remainder of *Silene* sect. *Otites*:

Silene sect. **Albopetalae** P. Panov, Compt. Rend. Acad. Bulg. Sci. 27: 1571. 1974.

This correction also affects Devtajov's (1987) inclusion of *Silene* sect. *Balcanosilene* in his treatment of the genus *Otites*, which requires the following new combination.

Otites sect. **Albopetalae** (P. Panov) Rabeler, comb. nov. *Silene* sect. *Albopetalae* P. Panov, Compt. Rend. Acad. Bulg. Sci. 27: 1571. 1974.—TYPE: *Otites roemeri* (Friv.) Holub.

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THE OCCURRENCE OF ANTHER SMUT, USTILAGO VIOLACEA S.L., ON STELLARIA BOREALIS (CARYOPHYLLACEAE) IN NORTH AMERICA

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INTRODUCTION

While working with members of the *Stellaria calycantha* (Ledeb.) Bong. complex (Rabeler 1986), I found several specimens of *Stellaria borealis* Bigelow which had enlarged reddish anthers. Further inspection revealed that these anthers contained spore masses of *Ustilago violacea* (Pers.) Roussel rather than pollen. I also discovered that, contrary to the information available from specimens at hand, this host-parasite pair had been reported only twice in North America (Rostrup 1891; Savile 1953); the intent of this paper is to correct that discrepancy.

Smut fungi of the genus *Ustilago* are known to attack many members of the Caryophyllaceae by replacing the contents of the ovary [e.g., in species of Alsinoideae and *Silene otites* (L.) Wibel] or the anthers (in species of Alsinoideae and Caryophylloideae[1]) with a spore mass (Durrieu & Zambettakis 1973). *Ustilago* has been reported on eight species and one hybrid of *Stellaria*: in Europe on seven species and one hybrid, in arctic North America on two species, and in Japan on one species (Zundel 1953; Lindeberg 1959; Conners 1967; Ginns 1986).

The taxonomy of the anther smuts found on Caryophyllaceae is complex and subject to various interpretations; see Deml and Oberwinkler (1982) for a summary. I follow Vanky (1985) in retaining the taxon of *Ustilago* occurring on *S. borealis* within *Ustilago violacea* and thus emphasize the intergradation in spore size among the three varieties that Savile (1953) recognized. If the apparent biological difference between those species infecting members of subfamily Alsinoideae and those infecting species of subfamily Caryophylloideae is accepted, this smut is recognized either as *U. violacea* var. *stellariae* (Sowerby) Savile (e.g., Savile 1953; Lindeberg 1959) or as *U. stellariae* (Sowerby) Liro (e.g., Durrieu & Zambettakis 1973). Deml and Oberwinkler (1982), who transferred the anther smuts infecting Caryophyllaceae to the genus *Microbotryum* Léveillé, emphasized the differences between these smuts and those infecting members of Poaceae; they recognized the *Stellaria* smut as *M. stellariae* (Sowerby) G. Deml & Oberw.

EFFECTS OF ANTHER SMUT

Several collections of *Stellaria borealis* examined included both infected and smut-free plants (noted as ± in specimen citations below). The leaves of some

[1] I follow Art. 19.3 of the *International Code* (Greuter et al. 1988) in using the autonym Caryophylloideae to designate the subfamily which includes the type of the family name, *Caryophyllus* Miller (=*Dianthus* L.).

infected plants are slightly smaller, but the most evident differences are found in the flowers. The flowers of infected plants are often slightly smaller than those of uninfected plants, a condition also reported in smut-infected *Dianthus* (Spencer & White 1951) and *Stellaria longipes* Goldie s.l. (Kevan & Parmelee 1972). The anthers are often nearly twice the size of uninfected anthers, dark red, and persistent (rather than deciduous) even in the oldest flowers on the plant. Spores are often found on other flower parts, giving the flowers a reddish cast that is often visible on recently collected herbarium specimens. Although not totally suppressed as in *Dianthus* (Spencer & White 1951), gynoecial development is interrupted. The styles are often shorter than those of non-infected plants, and all infected plants examined were devoid of capsules.

The fungus is probably dispersed by insects visiting the flowers; Kevan and Parmelee (1972) reported such dispersal in populations of *Stellaria longipes* in northern Canada. Since the smut infection prevents seed formation, it is likely that *Ustilago* operates as a local "population regulating factor" in a similar manner to that found by Jennersten et al. (1983) in *Ustilago*-infected populations of *Lychnis viscaria* L. (=*Viscaria vulgaris* L.) in Sweden.

OCCURRENCE OF USTILAGO VIOLACEA ON STELLARIA BOREALIS SUBSP. BOREALIS

The only previous reports of *Ustilago violacea* found on *Stellaria borealis* in North America were single occurrences in Alaska (Savile 1953) and Greenland (Rostrup 1891). Although Savile (1953) listed *S. calycantha* as the host, the collection that Savile cited (*Calder 5696*, BPI, DAOM) is actually *S. borealis*.

The occurrence of *Ustilago violacea* on *Stellaria borealis* is, as McCain and Hennen (1986) suggested could be the case for many pathogenic fungi, more common and widespread than any previous information would suggest (Fig. 1). The forty-two smut-infected collections of *S. borealis* subsp. *borealis* examined came from nine Canadian provinces/territories, Greenland, and three states of the U.S.A., i.e., widely scattered collections made throughout the North American range of the host (see Morton & Rabeler 1989; Fig. 2). The collections from New Hampshire (six collections made from 1886–1924) and Wyoming (one 1914 collection) appear to be the first reports of this host-parasite pair in the contiguous United States; there is no mention of anther smuts infecting *Stellaria* in the recent compendium *Fungi on Plants and Plant Products in the United States* (Farr et al. 1989). *Ustilago* has been infecting *S. borealis* for many years; the earliest collection seen was made in northern Manitoba in 1854 (*McTavish s.n.*, CAN).

Specimens examined ($^+$ - all plants infected; $^\pm$ - some plants infected; $^-$ - no plants infected). **Canada.** Alberta: N end of Cameron Lake, Waterton Lakes NP, 49°01'N, 114°01'W, 17 Aug 1980, *Rabeler 557* (MSC$^+$).—Manitoba: York Factory, 23 Jul 1854, *McTavish s.n.* (CAN$^\pm$).—Newfoundland: Southwest Gulch, NE of Summit of Bard Harbor Hill, 22 Aug 1925, *Fernald et al., Fl. NW Newfoundland 28188* (GH$^+$, PH$^+$).—Newfoundland/Labrador: Battle Harbour, 8 Jul 1892, *Waghorne HGSC 4769* (CAN$^+$), Jul 1935, *A. M. Ayre s.n.* (NFLD$^\pm$); Northwest Labrador, 17 Jul 1963, *Hustich & Kallio 460* (CAN$^\pm$); Head of Lake Tasisuak, Fraser Canyon, 100 km W of Nain, 0 m, 7 Aug 1973, *Shepherd & Matthews 2* (NFLD$^+$).—Northwest Territories: Mackenzie Dist., near Brintnell Lake, 62°5'N, 127°35'W, 3 Aug 1939, *Raup & Soper 9693* (A$^+$, CAN$^+$, RM$^+$, S$^\pm$, UBC$^+$); Nahanni NP, 61°09'N, 123°48'W, 524 m, 22 Jul 1976, *Talbot T6108-15* (DAO$^+$).—Nova Scotia: Victoria Co., Cliff above Gray Glen Brook, 14 Jul 1951, *Smith et al. 4436* (CAN$^+$, DAO$^+$).—Ontario: Kenora Dist., Riverbank, Jigsaw Island, Hudson Bay lowlands, 54°52'N, 85°45'W, 13 Jul

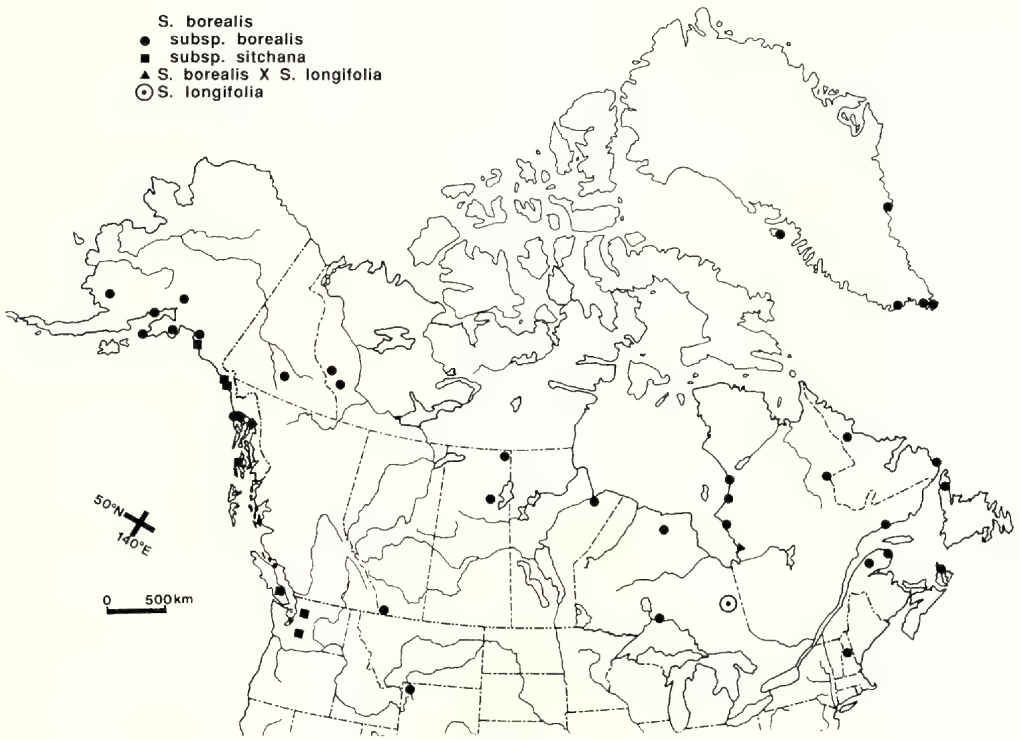

FIG. 1. Distribution in North America of smut-infected collections of *Stellaria borealis* subsp. *borealis* and subsp. *sitchana*, *S. borealis* × *S. longifolia*, and *S. longifolia*.

1958, *Baldwin 7611* (CAN$^+$, MTMG$^-$). Thunder Bay Dist., Schreiber, 48°45'N, 87°15'W, 30 Jun 1937, *Hosie et al. 621* (MT$^+$).—QUÉBEC: Duplessis Co., Knob Lake, Schefferville, 54°45'N, 66°40'W, 4 Aug 1963, *Hustich & Kallio 836* (CAN$^\pm$). Gaspe-Est Co., Gaspe Baisin, 24 Jul 1882, J. *Macoun s.n.* (MTMG$^+$). Gaspe-Ouest Co., foot of Mont Lyall, 31 Jul 1930, *Marie-Victorin et al. 33536* (GH$^+$, MT$^\pm$, RM$^\pm$). Nouveau-Québec: shore of Wiachewan River, Richmond Gulf, 56°15'N, 76°W, 17 Jul 1939, *Abbe et al. 3326* (CAN$^\pm$, DAO$^-$, DS$^-$, GH$^-$, MIN$^\pm$, PH$^-$, UC$^-$, US$^-$); granite hill S of Great Whale River, 13 Aug 1947, *Baldwin et al. 636* (CAN$^\pm$); 1 mi N of Saulaie, Great Whale River, 55°17'N, 77°46'W, 20 Aug 1970, *Brisson & Forest 22493* (DAO$^\pm$); Fort Georges, 53°53'N, 16-31 Jul 1944, *Dutilly & Lepage 12597* (GH$^+$). Saguenay Co., Ile aux Starlettes, Pashashibou River, 22 Jul 1960, *Desmarais 1932* (MT$^+$).—SASKATCHEWAN: Davin Lake, 1 mi W of Mile 46, Hwy 105, 56°52-53'N, 103°36'W, 4 Aug 1975, *Harms 22565* (DAO$^+$); near "Quillwort" Lake, S of Hasbala Lake, 59°54'N, 102°05'W, 30 Jul 1962, *Argus 948-62* (DAO$^+$, GH$^+$).—YUKON TERRITORY: Quiet Lake, Mile 55-60, [South] Canol Road, 4 Jul 1944, *Porsild & Breitung 11113* (CAN$^\pm$, GH$^+$, UC$^\pm$). **Denmark.** GREENLAND: Angmagssalik Dist., Sieraq, 65°56'N, 37°09'W, 27 Jul 1970, *Astrup & Kliim-Nielsen, G.B.U. 742* (MTMG$^\pm$). Disko Dist., South coast at Kigdlussah, 1 Aug 1932, *Grontved 386* (GH$^\pm$). Amitsuarssuk, 60°08'N, 44°45'W, 7 Aug 1967, *Hansen et al. G.B.U. 67-1984* (DAO$^\pm$, PH$^+$). Nupiluk, 60°46'N, 46°10'W, 100 m, 21 Jul 1962, *Hansen et al., Pl. Vasc. Groen. Exsic. 200* (COLO$^\pm$, DAO$^+$, MTMG$^\pm$, US$^+$). Kingna Jasinsak, 61°45'N, 1889, *N. Hartz s.n.* (GH$^\pm$). **U.S.A.** ALASKA: Kenai Peninsula: Seldonia, 12 Jul 1913, *R. F. Griggs s.n.* (US$^\pm$); NW end of Kenai Lake, 60°29'N, 149°48'W, 6 Jul 1951, *Calder 5696* (BPI$^+$, DAOM$^+$). Talkeetna, 11 Aug 1941, *Anderson 7700* (CAN$^+$, ISC$^+$, UTC$^+$); N shore of Lower Lake Nerka, Wood Tikchik State Park, 5 Aug 1990, *P. Caswell s.n.* ([ALA], HHH$^+$); Chichagof Island, Hoonah, 13 Jul 1932, *Norberg 200* (CAS$^+$, DS$^+$); Upper Seal River, Redoubt Bay, Big (Katnu) River delta, 60°39'N, 152°02'W, 18 Jul 1981, *Pogson 81-105* (ALA$^+$); terminus of Sheridan Glacier, NE of Cordova, 1965, *Tuthill S-13-3* (DS$^+$).—NEW HAMPSHIRE: Coos Co., Madison Spring, Mt. Madison, 12 Sep 1886, *T. O. Fuller s.n.* (NEBC$^\pm$); Boott's Spur, 1520 m, 22 Jul 1901, *Forbes 310* (PH$^\pm$); in a spring, Mt. Washington, 1520 m, 9 Aug 1902, *F. F. Forbes s.n.* (WIS$^+$); Alpine Garden, Mt. Washington, 5 Jul 1895, *J. R. Churchill s.n.* (NEBC$^+$, US$^+$), 19 Aug 1907, *Pease 10557* (NEBC$^+$); Hook above Alpine Garden, 1580 m, 24 Aug 1924, *Hotchkiss 70* (US$^+$).—WYOMING: Park Co., Woods by Yellowstone River, 17 Aug 1914, *Hunnewell 3076* (GH$^\pm$).

OCCURRENCE OF USTILAGO VIOLACEA ON STELLARIA BOREALIS SUBSP. SITCHANA

Ten smut-infected collections of *S. borealis* subsp. *sitchana* (Steudel) Piper were examined: seven from Alaska, two from Washington, and one from British Columbia; five of these were gathered since 1967. The occurrence of *U. violacea* on *S. borealis* subsp. *sitchana* from northern Washington [*Rabeler 467* (MICH, MSC) and *470*(MSC)] may represent the first collection of *Ustilago* on *Stellaria* in the Pacific Northwest; Shaw (1973) listed *U. violacea* as occurring in that region, but not on *Stellaria*.

Specimens examined ($^+$ - all plants infected; $^\pm$ - some plants infected; $^-$ - no plants infected). **Canada.** British Columbia: Vancouver Island, Dunsmuir Dist., Alluvial soil, Middle Nanaimo River Valley, 49°05'N, 124°16'W, 212 m, 2 Jul 1967, *Mueller-Dombois 63-5* (UBC$^\pm$). **U.S.A.** Alaska: Mendenhall, 30 Jun 1925, Anderson 139 (ISC$^+$); Prince of Wales Island, Craig, 31 Jul 1916, *Anderson 3015* (ISC$^+$); Eagle River, Juneau, 28 Jun 1940, *Anderson 6238* (ALA[2$^{\pm,+}$], CAN$^+$, DAO$^+$, GH$^+$, PH$^-$, RM[2$^+$], UTC$^\pm$, VT$^-$); coastal marsh, Hartney Bay, 60°30'N, 145°52'W, 16 Jul 1977, *Batten & Murphy 77-330* (ALA$^+$, UBC$^+$); S shore of Windham Bay, Tongass NF, T50S R75E S11, 20 Jul 1981, *Muller 4427* (WTU$^+$); Chichagof Island, Hoonah, 25 Jul 1932, *Norberg 228* (CAS$^-$, DS$^-$, GH$^+$, NY$^-$); Yakutat, 24 Jun 1916, *Walker & Walker 1056* (RM$^+$, US$^+$).—Washington: Pierce Co., Group Campsite 1, Sunshine Point Campground, Mt. Rainier NP, T15N R7E S34 SW1/4, 623 m, 31 Jul 1980, *Rabeler 470* (MSC$^\pm$). Snohomish Co., Ice Caves Trail, 1.2 km S of Federal Hwy 7, 24 km E of Verlot, Mt. Baker-Snoqualmie NF, T30N R10E S22 SW1/4, 30 Jul 1980, *Rabeler 467* (MICH$^+$, MSC$^+$).

OCCURRENCE OF USTILAGO VIOLACEA ON STELLARIA BOREALIS SUBSP. BOREALIS × S. LONGIFOLIA AND S. LONGIFOLIA

The ranges of *Stellaria borealis* subsp. *borealis* and *S. longifolia* Muhl. ex Willd. overlap in northern North America. These taxa occasionally hybridize, producing sterile triploid progeny that can be distinguished from both parents (Rabeler 1986; Morton & Rabeler 1989). This hybrid is common in Scandinavia (often referred to as either *Stellaria calycantha* × *longifolia* or *S. alpestris* Fries), and *Ustilago violacea* infection is known from there (Lindeberg 1959). The following specimen represents the first North American record.

Canada. Québec: Nouveau Québec: Buissons, East Main River, 52°15'N, 28-29 Aug 1944, *Dutilly & Lepage 13491* (GH$^+$).

Ustilago violacea has been reported on *S. longifolia* in Europe (Lindeberg 1959). Since I have not examined a large number of specimens of *S. longifolia*, I cannot offer any information on the range of this host-pathogen pair. The following specimen appears to be the first report of the host-parasite pair from North America.

Canada. Ontario: Cochrane Dist., Spring Trail, N shore of Lockett Lake, Greenwater Park, Clute Twp. Lot 28, Conc XII, 10 Jul 1972, *Bower 59* (OAC$^+$).

USTILAGO AND THE TAXONOMY OF THE STELLARIA CALYCANTHA COMPLEX

Besides the taxa mentioned above, Morton and Rabeler (1989) included *S. calycantha*, *S. crispa* Cham. & Schldl., and *S. obtusa* Engelm. as members of the *S. calycantha* complex. They found that, contrary to previous treatments, S. *borealis*

and *S. calycantha* were both morphologically and cytologically distinct. It has been suggested by some workers (e.g., Savile 1979) that the host distribution of parasitic fungi can be useful in resolving taxonomic problems of vascular plants. In the present case, the occurrence of *Ustilago* agrees with the recognition of *S. borealis* and *S. calycantha*; *Ustilago* is known from 52 collections of *S. borealis* but not from *S. calycantha*. A similar presence/absence case involves *S. borealis* subsp. *sitchana* and *S. crispa*. *Ustilago* is as yet unknown in *S. crispa*, although sympatric with it along the western North American coast from California to Alaska (see Morton & Rabeler 1989, Figs. 3 and 4, respectively).

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NEW SPECIES OF ASTERACEAE-HELIANTHEAE FROM LATIN AMERICA

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The active exploration of several regions of Mexico by personnel of the National Herbarium of Mexico and our field trips, during which we concentrated on collecting members of the Asteraceae, have resulted in the discovery of nine of the eleven new species described herein.

Two of the new species belong to the genus *Oteiza*, which was previously known only from two rare, seldom collected species. The morphology and generic affinities of *Oteiza* are discussed. The new species are described as outlined in Panero (1992).

Coreopsis davilae Panero & Villaseñor, sp. nov.—TYPE: MEXICO. Puebla: Summit of Cerro Tepoxtla Grande (a peak of the Filo de La Tierra Colorada range) just NW of the village of San Martín de Esperilla and S of Chacnopalan, 2650 m, 1 Nov 1991, *Panero, Dávila & Tenorio 2590* (holotype: MEXU!; isotypes: ENCB! MEXU! MICH! TENN! TEX! UC! US!). Fig. 1.

A *C. petrophiloide* inflorescentiis minoribus, capitulis majoribus, et habitu humili frutescenti differt.

Small shrubs 20–40 cm tall; stems terete, herbaceous parts glabrous or with a few moniliform trichomes, woody parts gray. Leaves opposite, pinnately veined; blades 1.5–5 cm long, 1.2–4 cm wide, smaller distally towards the capitulescence, rhombic in outline with two or three lobes at each side of the blade, the lowermost lobe larger and longer than the distal ones, adaxial surface glabrescent, green, abaxial surface glabrescent, creamy green, margins deeply dentate, apex acute to acuminate, base attenuate; petiole 0.6–2.5 cm long. Capitulescence a solitary head or of 3 heads arranged in a simple dichasium; peduncles 4–8 cm long, trichomes like those of the stems, purple-green. Heads heterogamous, radiate, hemispheric, 1–1.3 cm high, 1.4–1.8 cm wide (excluding ligules); receptacle 5.5–6 mm wide, flat. Phyllaries 20–26 in 4 graduated series; phyllaries of first and second series 4.5–6 mm long, 1–1.8 mm wide, appressed, herbaceous, lanceolate to linear, glabrous, green; phyllaries of third and fourth series 7–8.5 mm long, 4–4.5 mm wide, appressed, chartaceous, obovate to oblong, glabrescent, brown-orange with numerous black resin canals in the central portion of the phyllary, rimmed with yellow. Pales 6.3–6.8 mm long, 2–2.4 mm wide, oblong, shallowly conduplicate, not keeled, glabrescent, same color as innermost phyllaries, apex

FIG. 1. *Coreopsis davilae* (*Panero, Dávila & Tenorio 2590*). a. Habit. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Head (ligules not shown). (a, f, bar = 1 cm; b–e, bar = 1 mm.)

truncate. Ray flowers 11–15, corollas yellow-orange; ligule 1.4–2 cm long, 7–7.5 mm wide, oval, glabrous, veins on abaxial surface blackish, apex bifid, rounded; tube 2.2–2.5 mm long, sparsely puberulent, greenish yellow. Ray ovary 3.9–4.2 mm long, oblong to obovate, densely sericeous on edges, epappose. Disk flowers 45–65, hermaphrodite, corollas campanulate, yellow-orange with black resin canals running lengthwise along each side of the veins; throat 2.8–3 mm long, essentially glabrous; tube 2 mm long, glabrescent, greenish yellow; lobes 1–1.4 mm, deltate, glabrescent, yellow-orange rimmed with black resin canals; anthers 1.9–2.2 mm long, brown-black, appendages 0.6 mm long, oval to suborbicular; styles 4.5–5 mm long, yellow-orange with two black resin canals running lengthwise the style and abaxial surface of style branches, style branches 1.2–1.4 mm long, acute. Disk achene (immature) 3.2–3.5 mm long, 1–1.5 mm wide, oblong, densely sericeous on edges and central area of achene; pappus of two prominent awns 4.1 mm long. Chromosome number unknown.

Coreopsis davilae is known only from gypsum outcrops of the summits of Cerro Tepoxtla Grande and nearby Cerro Tres Encinos (or Tres Mogotes). At the type locality, the species is rare but at Cerro Tres Encinos it is abundant, growing in the crevices of rocks with *Coreopsis parvifolia* Blake, *Tridax palmeri* A. Gray, *Nolina* sp., and shrubby oaks.

Coreopsis davilae shares with *C. petrophiloides* B. L. Rob. & Greenm. of western Mexico a similar leaf shape and head morphology, although the heads of *C. davilae* are nearly twice as large as those of *C. petrophiloides*. The capitulescence structure is also helpful in distinguishing both species; *C. davilae* has a solitary head or a simple dichasium (3 heads), whereas *C. petrophiloides* typically has a monochasial thyrse of 6–30+ heads. Another distinguishing characteristic is habit; *C. davilae* is a low shrub no more than 40 cm tall, whereas *C. petrophiloides* is normally a taller and denser shrub 0.8–1.5 m tall.

The species name honors our good friend Dra. Patricia Dávila, chair of the Botany Department, U.N.A.M. Her interest in the area of Tehuacán is responsible for the successful project Flora of Tehuacán, which will result in a Flora for this botanically exciting area. Her desire to know and understand the vegetation of every corner of the valley of Tehuacán took us to the botanically unexplored Filo de La Tierra Colorada range, where we found this novelty and the beautiful *Viguiera davilae* (see below).

Oteiza mixtecana Villaseñor & Panero, sp. nov.—TYPE: MEXICO. Oaxaca: Mpio. Tamazulapan, Cerro Pericón al NW de San Pedro Nopala, 2660 m, *Tenorio, Dávila & Panero 18024* (holotype: MEXU!; isotype: MICH!). Fig. 2.

A *O. acuminata* capitulis minoribus, inflorescentiis majoribus congestioribusque, et foliis minoribus differt.

Perennial herbs 40–80 cm tall; stems terete, glabrous to sparsely puberulent, purple. Leaves opposite, triplinerved; blades 2–5.5 cm long, 0.7–2.5 cm wide, smaller distally towards the capitulescence, ovate, adaxial surface sparsely scabrous, shiny green, abaxial surface sparsely strigose, creamy green, margins entire to shallowly serrulate, sometimes with 4–7 mucros at each side of the blade, apex acuminate, base obtuse; petiole 1–4 mm long. Capitulescence of 9–25+ heads, dichasial-thyrsoid; peduncles 4–5 mm long, densely puberulent, greenish white. Heads heterogamous, radiate, narrowly campanulate to tubular, 1–1.2 cm high, 3–5 mm wide (excluding ligules); receptacle 1 mm long, 1 mm wide, conical. Phyllaries 9–13 in 4 graduated

FIG. 2. *Oteiza mixtecana*, *O. scandens*, and *Schistocarpha pedicellata*. a–f. *Oteiza mixtecana* (*Tenorio, Dávila & Panero 18024*). a–f. a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Head (ligules not shown). g–n. *Oteiza scandens* (*Panero & Campos 2745*). g. Flowering branch. h. Disk corolla. i. Outermost pale. j. Innermost pale. k. Ray corolla. l. Disk achene (immature). m. Disk achene (mature). n. Head (ligules not shown). o. *Schistocarpha pedicellata* (*Panero & Campos 2752*). o. Disk achene. (a, f, g, n, bar – 1 cm; b–e, h–m, o, bar = 1 mm.)

series, phyllaries of all series essentially identical in morphology differing only in size, 1.5–6.5 mm long, 1–2.5 mm wide, appressed, chartaceous to indurate, lanceolate to oblong, glabrescent, stramineous-green, distal 1/3 to 1/5 of phyllary herbaceous, appressed, green. Pales 5–6 mm long, 0.8–1.5 mm wide, narrowly oblong, flat not conduplicate, glabrescent, stramineous-green, apex rounded to acute. Ray flowers 5–6, pistillate, corollas yellow-white to greenish white; ligule 5.5–6 mm long, 3–4 mm wide, oval, glabrous, veins on abaxial surface somewhat greenish, apex conspicuously trifid, truncate; tube 2.5 mm long, sparsely puberulent, greenish yellow; style 4.2–4.5 mm long, style branches 0.5–0.6 mm long, acute without appendage. Ray achene 2 mm long, obconical, glabrous, black; pappus of 17–26 awns or bristles of different lengths, 1.8–2.7 mm long, stramineous, caducous, the pappus arising from a ring smaller in circumference than the top of the achene. Disk flowers 8–13, hermaphrodite, protruding 4–5 mm beyond pales, corollas campanulate, yellow-green with orange resin canals running lengthwise along each side of the veins and splitting at the lobe sinus with 5 additional resin canals running lengthwise the throat from the tip of the lobes down to the junction of the throat and the tube; throat 3.8–4.2 mm long, 0.5–0.7 mm wide at base, 1.2 mm wide at top, essentially glabrous; tube 1.6–1.9 mm long, moderately puberulent, greenish yellow; lobes 1.5 mm long, deltate, glabrous abaxially; anthers 1.4–1.6 mm long, yellow-green, appendages 0.5 mm long, lanceolate, yellow; styles 5.5 mm long, yellow, style branches 0.5–0.7 mm long, acute, without appendages. Disk achene like ray achene. Chromosome number unknown.

Additional Specimens Examined. **Mexico.** Oaxaca: Mpio. Tamazulapan, Cerro Pericón, al NW de San Pedro Nopala, 2400–2600 m, 21 Oct 1984, *Tenorio et al. 7863* (MEXU); Mpio. San Pedro Topiltepec, Santa María Tiltepec, 2420 m, 4 Oct 1990, *Cruz 264* (TEX).

Oteiza mixtecana is a rare species of the dry oak and pine-oak forest of Cerro Pericón of northwestern Oaxaca. The mountain range where the type collection was gathered has been totally deforested and most of the topsoil has been eroded, so the survival of *O. mixtecana* in this area is doubtful. Given the scattered individuals of *Erythrina* L. and *Furcraea* Vent. that dot the barren hills, *O. mixtecana* must have grown in a distinctive oak forest. Other unusual and rare species of Asteraceae found in the area are: *Tridax luisana* Brandegee, *Acourtia tenoriensis* B. Turner, *Senecio purpusii* Brandegee, and *Coreopsis oaxacensis* B. Turner.

Oteiza mixtecana shares with *O. acuminata* La Llave of central Mexico a similar disk and ray corolla color, conical receptacles, a caducous pappus of multiple awns borne on a ring, large nectaries (especially evident in young flowers just before anthesis), and a graduated involucre composed of mostly chartaceous, imbricate phyllaries. The major difference between the two species is the size and arrangement of the heads, which in *O. acuminata* are approximately two to three times larger than those of *O. mixtecana*. The capitulescence of O. *mixtecana* is composed of numerous, tightly packed heads, whereas in *O. acuminata* the heads are borne in longer peduncles and the capitulescence is normally smaller ranging from 3 to 18 heads. The larger leaves of *O. mixtecana* are half as large as those of *O. acuminata*. The relationship of these two species to the other two members of the genus is discussed below.

Oteiza scandens Panero & Villaseñor, sp. nov.—Type: Mexico. Oaxaca: Km 134.5 of the road Oaxaca–Puerto Angel, 2450 m, 16 Feb 1992, *Panero & Alvaro*

Campos 2745 (holotype: MEXU!; isotypes: ENCB! K! MA! MEXU! MICH! MY! TENN! TEX! UC! US!). Fig. 2.

A *O. ruacophila* capitulis majoribus hemisphaericis et inflorescentiis foliisque majoribus differt.

Scandent shrubs or vines 1–8 m long; stems terete with a few striations, herbaceous parts sparsely puberulent, purplish green, woody parts gray. Leaves opposite, triplinerved; blades 9.5–13 cm long, 6.5–10 cm wide, smaller distally towards the capitulescence, ovate, adaxial surface sparsely scabrous to strigose, green, abaxial surface essentially glabrous, slightly lighter in color than adaxial surface, margins serrulate, the tip of each serration terminated by a prominent mucro, apex acuminate, base obtuse and cuneately narrowed into petiole; petiole 3–6 cm long. Capitulescence of 9–60+ heads, dichasial-thyrsoid; peduncles 5–15 mm long, sparsely puberulent, green. Heads heterogamous, radiate, hemispherical, 1–1.3 cm high, 0.8–1 cm wide (excluding ligules); receptacle 2 mm long, 2 mm wide, conical. Phyllaries 18–24 in 3 graduated series; phyllaries of first series 3.8–5 mm long, 2–3 mm wide, appressed, indurate, ovate, glabrescent, stramineous-green, distal 1/2 to 1/3 of phyllary herbaceous, appressed, green; phyllaries of second series 7–8 mm long, 2–2.5 mm wide, appressed, chartaceous to slightly indurate, ovate to lanceolate, glabrescent, stramineous-green, distal 1/5 of phyllary herbaceous, appressed, green; phyllaries of third series 0.8–1 cm long, 1.5–1.8 mm wide, appressed, indurate with essentially no herbaceous apex, stramineous-green, glabrous, narrowly lanceolate to linear. Pales 6 mm long, 1–1.5 mm wide, outermost pales narrowly oblong, innermost pales deeply trilobed or acicular, flat not conduplicate, glabrescent, stramineous-green, apex rounded to acute. Ray flowers 10–15, pistillate, corollas white; ligule 1–1.2 cm long, 4–6 mm wide, oval to oblong, glabrous, veins on abaxial surface somewhat purplish white, apex conspicuously trifid, truncate; tube 4–4.5 mm long, sparsely puberulent, greenish yellow; style 5 mm long, style branches 0.8–1 mm long, acute without appendage. Ray achene 1.5–2.5 mm long, obconical, glabrous, black; pappus of 16–30 awns or bristles of different lengths, 0.8–3.5 mm long, stramineous, caducous, the pappus arising from a ring smaller in circumference than the top of the achene. Disk flowers 40–60, hermaphrodite, protruding 4–5 mm beyond pales, corollas narrowly campanulate to tubular, yellow with orange resin canals running lengthwise along each side of the veins and splitting at the lobe sinus, with 5 additional resin canals running lengthwise from the tip of the lobes down to the junction of the throat and the tube; throat 5 mm long, 0.8–1 mm wide at base, 1.2 mm wide at top, essentially glabrous; tube 2 mm long, moderately puberulent, greenish yellow; lobes 0.6–0.8 mm long, deltate, moderately puberulent abaxially; anthers 1.6–2 mm long, yellow-green, appendages 0.5 mm long, lanceolate, yellow; styles 5 mm long, yellow, style branches 1 mm long, acute, without appendages. Disk achene like ray achene. Chromosome number: $n = 17$.

Oteiza scandens is known only from the type collection. The species is very conspicuous because of it scandent habit and numerous heads with large white ligules and bright yellow disk flowers, reminiscent of scandent individuals of *Montanoa atriplicifolia* (Pers.) Sch.-Bip. It grows in rich, mesic cloud forest of the Sierra de Miahuatlán, a part of the Sierra Madre del Sur of Oaxaca. The type locality is dominated by trees of *Alnus* Mill., *Carpinus* L., *Ulmus* L., *Cheiranthodendron* Kuntze, and *Buddleia* L. among many others. As is true of many of the other species here described, the habitat of *O. scandens* has been destroyed, and only a few plants remain at the type locality.

Oteiza scandens shares with *O. ruacophila* (Donn. Smith) Fay a similar scandent habit, a conical receptacle, large white ligules, a distinctive graduated involucre of mostly chartaceous phyllaries, and obconical achenes with a pappus of caducous awns. *Oteiza scandens* differs from *O. ruacophila* by its larger, hemispherical heads (campanulate in *O. ruacophila*), larger leaves, and oblong to trilobed pales (narrowly lanceolate to acicular in *O. ruacophila*).

With the two species of *Oteiza* described in this paper, the total number of species recognized in the genus grows to four. Within *Oteiza*, two clear lineages can be identified based on gross morphology and habitat preference. *Oteiza acuminata* and *O. mixtecana* are perennial herbs from dry oak or xerophytic forests, and have greenish yellow ray corollas and narrowly campanulate heads; *O. ruacophila* and *O. scandens* are vines in cloud forest or mesic oak forest, and have white ray corollas and campanulate to hemispherical heads. The four species share conical receptacles, caducous pappi of multiple awns, and highly graduated involucres composed of mostly chartaceous phyllaries. This combination of characters is not found in any of the purportedly related genera of *Oteiza*.

Oteiza has been traditionally allied to *Perymenium* Schrad. because of their superficially similar achene pappus morphology and duration. *Oteiza* differs from *Perymenium*, however, on several notable characteristics, namely, yellow anthers, conical receptacles, and achenes that are obconical and not compressed as in *Perymenium*.

The achene and ray corolla morphology of *Oteiza* is typical of subtribe Galinsoginae (sensu Robinson 1981). Based on disk flower microcharacters and head morphology, the genus has been recently allied to *Schistocarpha* Less. by Robinson (1979). *Oteiza* and more specifically its white ligule species resemble, albeit superficially, some species of *Schistocarpha* because of their graduated involucres with chartaceous phyllaries and pappus. The two genera can be easily separated by the disk achene pappus, which in *Oteiza* is composed of multiple caducous awns of different size that rarely exceed the base of the disk corolla throat. *Schistocarpha*, however, has a pappus of somewhat caducous awns or bristles that are mostly equal in length and normally are as long or slightly longer than the throat. Another important difference between the two genera is the apical morphology of the achene, more specifically, where the pappus is inserted. In *Oteiza* the pappus is borne from a ring which becomes less evident as the achene matures and plumps up, whereas in *Schistocarpha* the pappus is borne from a somewhat similar ring which, however, is as wide as the apical diameter of the achene and is made more evident by the conspicuous constriction of the achene immediately below the pappus.

Oteiza might be confused with *Alepidocline* S. F. Blake (sensu stricto: *A. annua* and *A. breedlovei*) because of their similar pappus. *Oteiza* differs from *Alepidocline* in having a mostly suffruticose habit (annuals in *Alepidocline*), and paleaceous, hemispherical or campanulate heads (epaleaceous and urceolate in *Alepidocline*).

Perymenium tehuacanum Villaseñor & Panero, sp. nov.—TYPE: MEXICO. Puebla: Mpio. de Totoltepec, 7 km al NW de Santa Cruz Nuevo, por el camino a San Juan Ixcaquistla, 1720 m, 21 Aug 1980, *González-Medrano, Jaramillo & Villaseñor 1236* (holotype: MEXU!; isotypes: MICH! TEX!). Fig. 3.

A *P. glanduloso* capitulis majoribus, pedunculis longioribus, phyllariis lanceolatis apicibus patentibus herbaceis, et foliis majoribus differt.

Small shrubs 1 m tall, stems terete, herbaceous parts sparsely hirsute with stipitate and sessile glandular trichomes, greenish brown, woody parts brown.

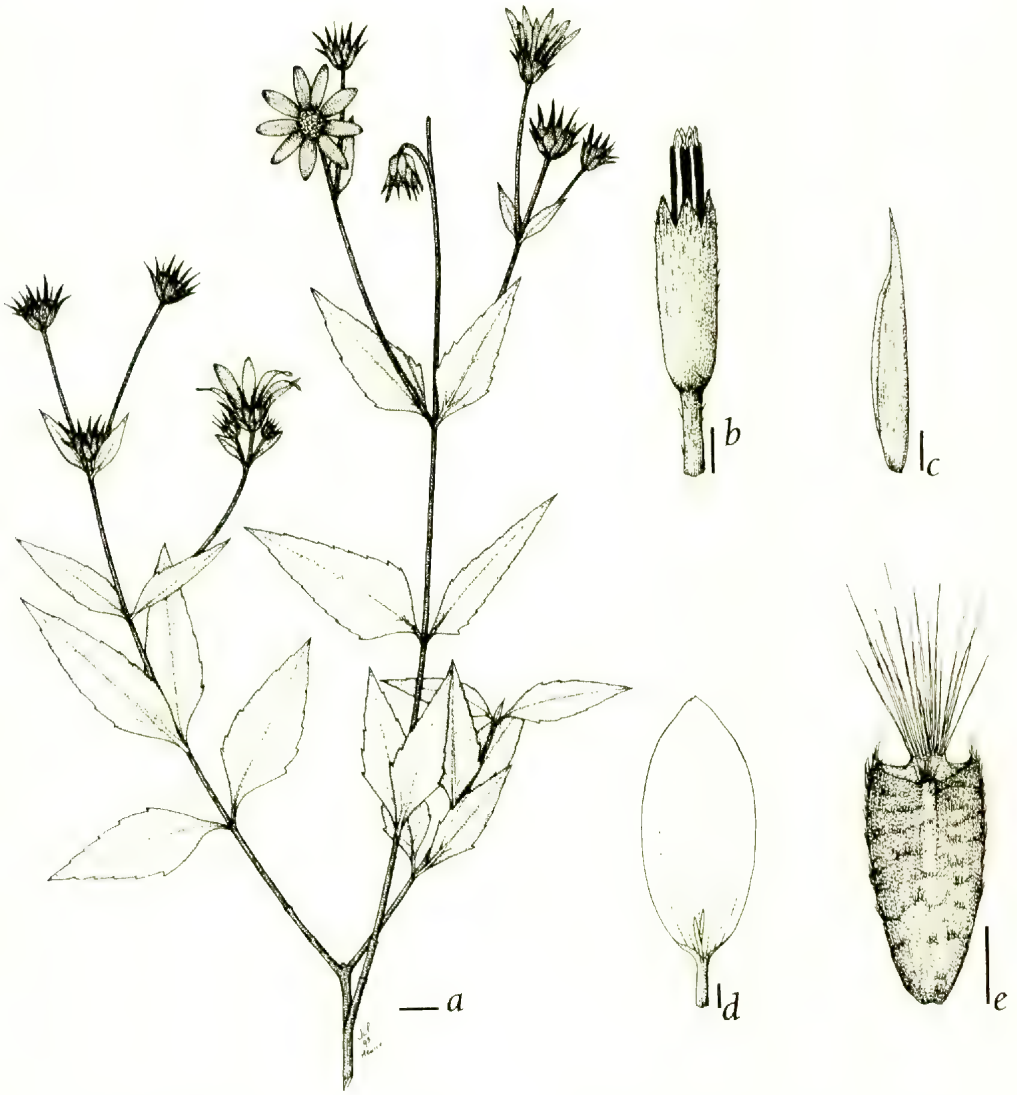

FIG. 3. *Perymenium tehuacanum* (*Medrano, Jaramillo & Villaseñor 1236*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. (a, bar = 1 cm; b–e, bar = 1 mm.)

Leaves opposite, triplinerved; blades 2–5.5 cm long, 0.6–2.5 cm wide, smaller distally towards the capitulescence, ovate, adaxial surface sparsely scabrous with stipitate glandular trichomes, light green, abaxial surface sparsely strigose with sessile and stipitate glandular trichomes, creamy green, margins dentate to entire, apex acuminate, base obtuse to attenuate; petiole 0.2–1 cm long. Capitulescence of 3–18 heads, dichasial-thyrsoid; peduncles 0.8–5 cm long, light green. Heads heterogamous, radiate, broadly campanulate, 0.8–1.4 cm high, 0.7–1 cm wide (excluding ligules); receptacle 4–5 mm wide, flat. Phyllaries 14–18 in 2 to 3 subequal series; phyllaries of first series 6–8 mm long, 2.5–3 mm wide, lanceolate, basal half of phyllary indurate, appressed, minutely hirsute and glandular, stramineous, distal half of phyllary herbaceous, spreading, sometimes slightly twisted, sparsely hirsute and glandular; phyllaries of second and third series 0.8–1.4 cm long, 1.5–3 mm wide, narrowly lanceolate, pubescence and color as in first series. Pales 6.5–8.5 mm long, 1.4–1.8 mm wide, shallowly conduplicate, not keeled, glabrescent

with a few stipitate glandular trichomes, basal half stramineous, distal half and apex stramineous-yellow, apex acuminate, erect to spreading. Ray flowers 7–10, pistillate, corollas golden-yellow; ligule 1–1.2 cm long, 4.5–5.5 mm wide, oval to oblong, sparsely puberulent on abaxial surface, apex shallowly trifid, round; tube 2–2.3 mm long, sparsely puberulent, greenish yellow; style 2 mm long, yellow, style branches 1.5 mm long, acute. Ray achene 3.7–4.2 mm long, 1.8–2.2 mm wide, oblong, triquetrous, sparsely to moderately sericeous, pubescence not uniform but concentrated as tufts on achene wall protrusions, greenish black; pappus of 14–18 somewhat caducous awns of different lengths, 1.5–3.5 mm long. Disk flowers 20–27, hermaphrodite, not exceeding the pales, corollas campanulate, yellow with orange resin canals; throat ca 3 mm long, ca 1.2 mm wide at base, ca 1.5 mm wide at top, glabrescent; tube 1.4–1.5 mm long, sparsely puberulent, yellow; lobes ca 0.8 mm long, deltate, glabrous abaxially; anthers 2 mm long, black, appendages 0.5 mm long, ovate, yellow; styles 4–4.5 mm long, style branches 1.2–1.4 mm long, acuminate. Disk achene 3.4–3.7 mm long, 1.3–1.5 mm wide, ovate, biconvex to prismatic, pubescence and pappus as in ray achene. Chromosome number unknown.

Perymenium tehuacanum is known only from the type collection, gathered along intermittent river canyons of the southern basin of the valley of Tehuacán.

Perymenium tehuacanum shares with *P. glandulosum* Brandegee and *P. cornutum* Brandegee a similar glandular herbage otherwise unknown in *Perymenium* (Fay 1978). The most distinctive characteristic of *P. tehuacanum*, however, is the involucre, composed of spreading, lanceolate phyllaries, which is unique in *Perymenium*.

Verbesina badilloi Panero, sp. nov.—TYPE: VENEZUELA. Mérida: 38 km S of Estanquez on rd to Canaguá, 2550 m, 2 Dec 1991, *Panero, Benítez de Rojas & Badillo 2685* (holotype: MY!; isotypes: COL! MA! MER! MEXU! MICH! TENN! TEX! UC! US! VEN!). Fig. 4.

A *V. tachirensi* capitulis majoribus, corollis florum radii discique majoribus, et floribus disci paucioribus differt.

Shrubs 3–4 m tall; stems terete, herbaceous parts densely tomentose to velutinous, pale green, woody parts light brown to gray. Leaves alternate, the larger ones asymmetrical, pinnately veined; blades 2–38 cm long, 2–16 cm wide, smaller distally towards the capitulescence, those associated with the capitulescence conspicuously smaller than the cauline leaves, elliptical, adaxial surface moderately minutely hirsute, green, abaxial surface moderately velutinous, creamy green, veins conspicuously outlined against background, sericeous, white-green, margins shallowly crenate with prominent mucros, apex acuminate, base attenuate; petiole 1–4 cm long. Capitulescence of 15–60+ heads, monochasial-thyrsoid; peduncles 0.5–4.5 cm long, densely pubescent. Heads radiate, campanulate, 1.2–1.4 cm high, 8 mm wide (excluding ligules); receptacle 4–5 mm wide, flat. Phyllaries 4–6 in 1 series, 4–12 mm long, 2.5–5 mm wide, appressed, herbaceous, oblong, sparsely to moderately velutinous to puberulent, somewhat rugose with transversal striations especially on the base, pale green suffused with dark green areas especially on edges and striations. Pales 10–11 mm long, 3.8–5 mm wide, oblong, conduplicate, moderately puberulent, basal half of pale green, distal half dark green to black, apex acute and spreading. Ray flowers 3, corollas white, pistillate; ligule 9–11 mm long, 4–6 mm wide, oblong, moderately puberulent abaxially, apex conspicuously trifid, tube 2.2–2.5 mm long, moderately to densely puberulent; style 4–4.5 mm long,

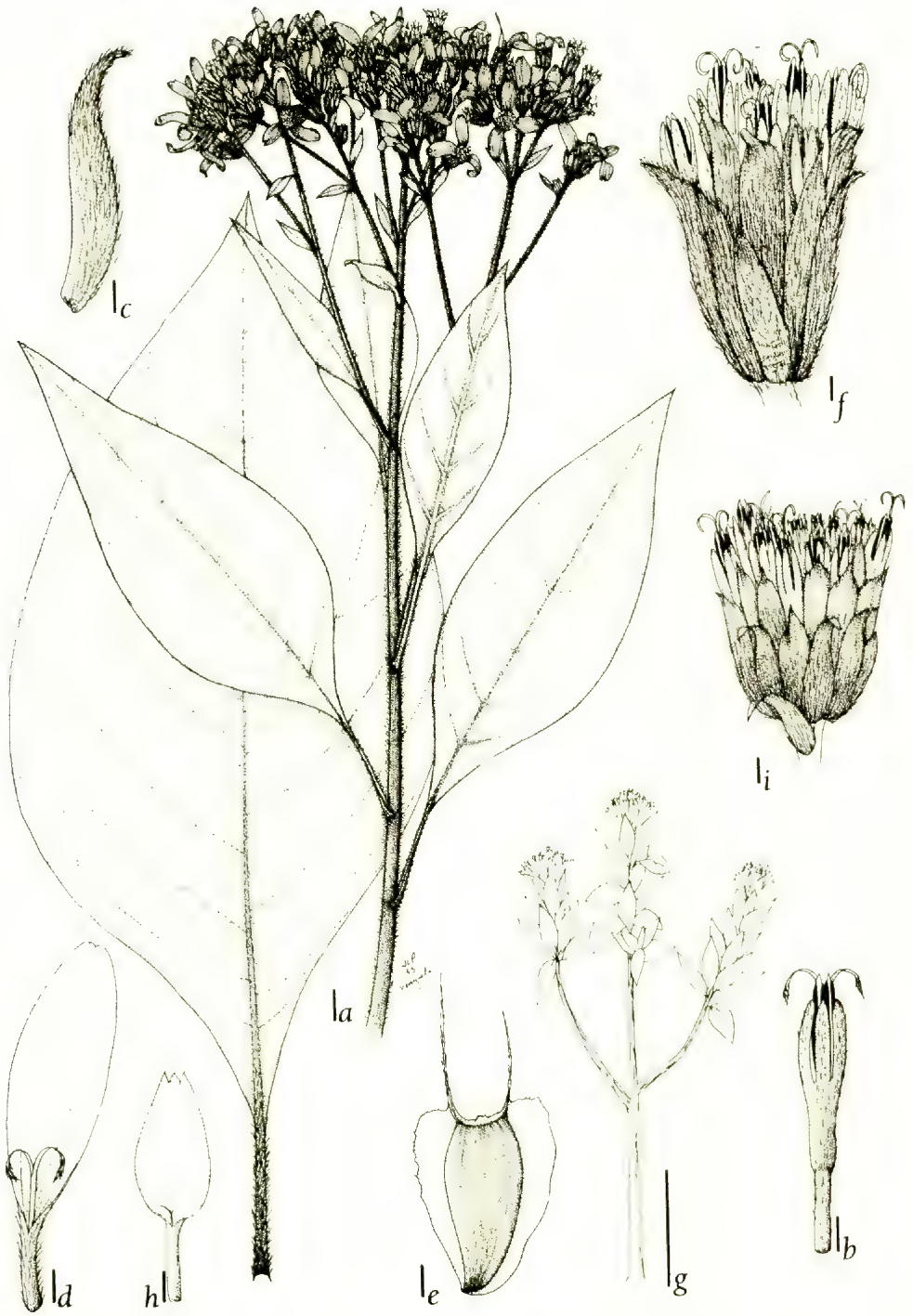

FIG. 4. *Verbesina badilloi* and *V. tachirensis*. a–g. *Verbesina badilloi* (*Panero, Benítez de Rojas & Badillo 2685*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Head (ligules not shown). g. Habit. h, i. *Verbesina tachirensis* (*Steyermark 57149*). h. Disk corolla. i. Head (ligules not shown). (a, bar = 1 cm; b–f, h, i, bar = 1 mm; g, bar = 1 m.)

white; style branches 1.5–2 mm long, white. Ray achene 5.5–6 mm long, 4–4.5 mm wide (including wings), flat, obovate, glabrescent, brownish black, pappus of two awns 3–3.2 mm long. Disk flowers 12–18, corollas white and black, hermaphrodite; throat 1.8–2.2 mm long, oblageniform, moderately puberulent, distal half of throat black, basal half white; tube 1.6–2 mm long, densely puberulent, white; lobes 2.5–2.8 mm long, sparsely puberulent on abaxial surface, abaxial surface black, adaxial surface white; anthers 2–2.2 mm, black, appendages 0.6 mm long, black; style 5.5–7 mm long, white, style branches 1.5–1.8 mm long, acute with prominent appendages. Disk achene like ray achene. Chromosome number: $n = 17$.

Additional Specimens Examined. **Venezuela**. Mérida: Bosques densos y húmedos entre San Isidro Alto y El Molino, 2200–2400 m, 2 Dec 1972, *Badillo 5835* (MY-3); same locality and date as type specimen, *Benítez de Rojas et al. 4429* (MY).

Verbesina badilloi occurs in the cloud forest of the southern escarpment of the Andean range of Mérida. Sadly, the native flora of the area has been nearly destroyed except for a few places along deep ravines, where the original vegetation, including *V. badilloi*, still persists. The survival of this species clearly depends on the conservation of these remnants of cloud forest.

Verbesina badilloi shares with *V. negrensis* Steyerm., *V. tachirensis* Steyerm., *V. laevifolia* S. F. Blake, and *V. acuminata* DC. a similar disk corolla morphology, which is unique in the genus. All these species have deeply dissected disk corolla lobes, which in some species measure up to two-thirds of the total length of the throat. *Verbesina badilloi* differs from *V. negrensis*, *V. acuminata*, and *V. laevifolia* in having broadly elliptical leaves with dull green adaxial surfaces and pubescent abaxial surfaces; the last three species have lanceolate to narrowly ovate leaves with dark greenish purple, shiny, resinous, and glabrescent adaxial surfaces and mostly glabrous abaxial surfaces. *Verbesina badilloi* shares with *V. tachirensis* a similar capitulescence structure, head and leaf morphology, and herbage pubescence. Furthermore, the two species have deeply dissected disk corollas with lobes that are black abaxially (a characteristic also shared with *V. acuminata*). *Verbesina badilloi* differs from *V. tachirensis* in having larger heads with ray and disk flowers, pales, achenes, and phyllaries that are twice as large or larger than those of *V. tachirensis*. *Verbesina badilloi* differs further from *V. tachirensis* in having more disk flowers per head and three ray flowers as opposed to four to six typical of *V. tachirensis*. In addition, the heads of *V. badilloi* are campanulate to cylindrical, whereas those of *V. tachirensis* are oblong to slightly hemispherical.

The specific epithet honors Dr. Victor Manuel Badillo, indefatigable student of the Venezuelan Flora and the family Asteraceae.

Verbesina hygrophila Panero & Villaseñor, sp. nov.—Type: Mexico. Durango: 14 km E of Canelas on rd to Santiago Papasquiaro, 2180 m, 28 Aug 1991, *Panero, González & Acevedo 2253* (holotype: MEXU!; isotypes: CIIDIR! MICH! TEX! US! UC!). Fig. 5.

A *V. synoti* inflorescentiis majoribus, phyllariis paleisque nigrescentibus, et foliis magnis ovatis vel suborbicularibus differt.

Shrubs 2–3 m tall, stems terete, herbaceous parts glabrous or glabrescent, purplish green, woody parts gray. Leaves opposite, triplinerved; blades 7–20 cm long, 2.5–13.5 cm wide, smaller distally towards the capitulescence, broadly ovate to suborbiculate, adaxial surface sparsely scabrous, green, abaxial surface velutinous, creamy green, veins outlined against background, velutinous-sericeous, white-green, margins serrulate, apex acuminate, base obtuse; petiole 3–16 cm long,

FIG. 5. Ver*besina hygrophila* and *V. papasquiara*. a–g. *Verbesina hygrophila* (*Panero, González & Acevedo 2253*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Head (ligules not shown). g. Habit. h–n. *Verbesina papasquiara* (*Panero, González & Acevedo 2264*). h. Flowering branch. i. Disk corolla. j. Pale. k. Ray corolla. l. Disk achene. m. Head (ligules not shown). n. Habit. (a, h, bar = 1 cm; b–f, i–m, bar = 1 mm; g, n, bar = 1 m.)

winged. Capitulescence of 30–200+ heads, monochasial-thyrsoid; peduncles 3–8 mm long, sparsely to moderately puberulent. Heads radiate, campanulate, 1–1.2 cm high, 0.8–1 cm wide (excluding ligules); receptacle 1–1.5 mm wide, flat. Phyllaries 8–10 in 1–2 series, 1.5–4 mm long, 0.7–1 mm wide, appressed, herbaceous, narrowly lanceolate, sparsely puberulent, dark green drying black. Pales 5.5 mm long, 2 mm wide, oblong to narrowly lanceolate, shallowly conduplicate, glabrous or sparsely puberulent, dark green drying black, apex acute, erect. Ray flowers 3–4, corollas yellow-orange, pistillate; ligule 7–8 mm long, 4.2–4.6 mm wide, oval, apex trifid, round; tube 1.5 mm long, sparsely puberulent; style 3.5 mm long, yellow; style branches 1.2–1.5 mm long, yellow. Ray achene 4.3–4.6 mm long, 2–2.4 mm wide (including wings), flat, obovate, glabrous, stramineous-green, pappus of two awns 2.4 mm long. Disk flowers 9–13, corollas yellow-orange, hermaphrodite; throat 5 mm long, narrowly campanulate, sparsely puberulent or glabrous; tube 2 mm long, glabrescent, greenish yellow; lobes 1.2–1.4 mm long, deltate, sparsely puberulent on abaxial surface; anthers 2.3–2.5 mm long, black, appendages 0.6 mm long, lanceolate, black; style 8 mm long, yellow, style branches 1.8–2.2 mm long, tapered with prominent appendages. Disk achene slightly larger than ray achene. Chromosome number: $n = 17$.

Verbesina hygrophila shares with *V. papasquiara*, *V. pauciflora* Hemsl., and *V. synotis* S. F. Blake opposite leaves, essentially glabrous stems, yellow-orange corollas, and a small number of disk flowers per head. In addition, all these species appear to be endemic to the pine-oak forest of the Sierra Madre Occidental of Durango, Sinaloa, and Chihuahua. *Verbesina hygrophila* differs from these species in having large, broadly ovate to suborbicular leaves and dark green to black phyllaries and pales; other differences among these species are summarized in the following key.

1. Leaves with entirely winged petioles, auriculate at base.
   2. Heads with 5–13 disk flowers.
      3. Phyllaries dark green drying black; blades broadly ovate to suborbicular; heads with 9–13 disk flowers. *V. hygrophila.*
      3. Phyllaries light green, drying stramineous-green; blades ovate; heads with 5–7 disk flowers. *V. synotis.*
   2. Heads with 18–25 disk flowers. *V. papasquiara.*
1. Leaves with partially winged petioles, not auriculate at base.
   4. Heads radiate, with 18–25 disk flowers. *V. papasquiara.*
   4. Heads discoid, with 7–10 disk flowers. *V. pauciflora.*

Verbesina hygrophila is known only from the type collection. The specific epithet refers to the fact that the single population found was growing along creeks in the shade of mesic pine-oak forest.

Verbesina lapazii Panero, sp. nov.—TYPE: BOLIVIA. La Paz: Prov. Nor Yungas, de Coroico 12 km hacia Coripata, 2050 m, 11 Apr 1990, *Beck 17629* (holotype: US!; isotype: LPB). Fig. 6.

A *V. leucactinota* capitulis majoribus, floribus radii discique majoribus et foliis integris differt.

Shrubs 3 m tall; stems terete, noticeably nerved when dry, herbaceous parts glabrous, green, woody parts unknown. Leaves alternate, pinnately veined; blades 10–25 cm long, 3.5–10 cm wide, slightly smaller distally towards the capitulescence, ovate, adaxial surface sparsely strigose to hirsute, abaxial surface moderately hirsute to villous, especially on veins, veins creamy white to tan and clearly

outlined against green background, margins entire to shallowly crenate with regularly spaced mucros at each side of the blade (ca 1 per cm), apex acuminate, base obtuse and attenuate into winged petiole; petiole 6–8.5 cm long, winged and auriculate at base. Capitulescence of 20–200+ heads, monochasial-thyrsoid; peduncles 0.6–1.2 cm long, sparsely puberulent, green. Heads heterogamous, radiate, campanulate, 5–5.5 mm high, ca 5 mm wide (excluding ligules), receptacle 2 mm long, flat. Phyllaries 9–12 in 2 graduated series; phyllaries of first series 1.8–2.2 mm long, 1–1.2 mm wide, appressed, mostly herbaceous, ovate, glabrescent, green; phyllaries of second series 4–4.3 mm long, 1.5–1.7 mm wide, appressed, obovate, glabrescent, basal half of phyllary stramineous, distal half green suffused with black. Pales ca 4.2 mm long, 1.5–1.8 mm wide, obovate, shallowly conduplicate, sparsely puberulent, stramineous green, distal half of pale suffused with black, apex broadly acute. Ray flowers 5–7, pistillate, corollas white; ligule 4.5–5 mm long, ca 2 mm wide, oblong, glabrescent on abaxial surface, apex trifid, round to truncate; tube 1.8–2 mm long, sparsely puberulent, greenish white; style 2 mm long, white, style branches 0.7–0.8 mm long, acute without appendage. Ray achene (immature) ca 2.5 mm long, obconical, essentially glabrous, black; pappus of two awns 2.5 mm long. Disk flowers 25–35, hermaphrodite, protruding 1–2 mm beyond pales, corollas tubular to narrowly campanulate, white; throat 1.8–2.2 mm long, 0.6 mm wide at base, 1.1 mm wide at top, sparsely puberulent, pubescence somewhat denser at base; tube 1 mm long, sparsely puberulent, greenish white; lobes 0.5 mm long, deltate, glabrous abaxially; anthers ca 1.5 mm long, black, appendages 0.2 mm long, ovate, black; styles 2 mm long, white, style branches 1.3–1.5 mm long, acute, without appendages. Disk achene like ray achene. Chromosome number unknown.

Additional Specimens Examined. **Bolivia**. La Paz: Prov. Nor Yungas, 10.2 km SW of Yolosa on rd to Chuspipata, ca 20 km NE of Chuspipata, 5 Apr 1984, 1700 m, *Solomon & Uehling 12239* (US); Hwy La Paz-Coroico, 7.3 km from Coroico, 1800 m, 31 Mar 1977, *Boeke 1421* (US).

Verbesina lapazii shares with the white-flowered, pinnately-leaved species of *Verbesina* small heads, white corollas, large capitulescences, alternate leaves, and a perennial or weakly shrubby habit. It differs from this group of species in having entire leaves (also seen in some populations of *V. turbacensis* H. B. K., *V. quetamensis* Olsen, *V. sararensis* Cuatrec., and *V. exalata* Steyerm.). *Verbesina lapazii* might be confused with the sympatric *V. leucactinota* B. L. Rob. because of their similar, massive capitulescences. It can be easily separated from this species by several features of the head and disk corolla. In *V. lapazii* the heads are campanulate and larger than those of *V. leucactinota*. In addition, the heads of *V. lapazii* have fewer disk flowers than those of *V. leucactinota*. Another important difference between both species is the length of the disk corolla lobes, which in *V. lapazii* are half as long as those of *V. leucactinota*. The most discrete difference between the two species is the leaf blade, which in *V. lapazii* is ovate and unlobed but in *V. leucactinota* is deltate in outline and pinnately lobed. *Verbesina lapazii* may also be confused with *V. semidecurrens* Kuntze because of its similar auriculate leaf bases. *Verbesina lapazii* is easily separated from *V. semidecurrens* by its campanulate heads (hemispherical in *V. semidecurrens*) with half as many disk flowers and graduated involucres with ovate to oblong, glabrescent phyllaries. In *V. semidecurrens* the involucre is not graduated, and the phyllaries are more numerous, lanceolate, and moderately villous. In addition, the pale apex of *V. lapazii* is acute, whereas in *V. semidecurrens* it is acuminate.

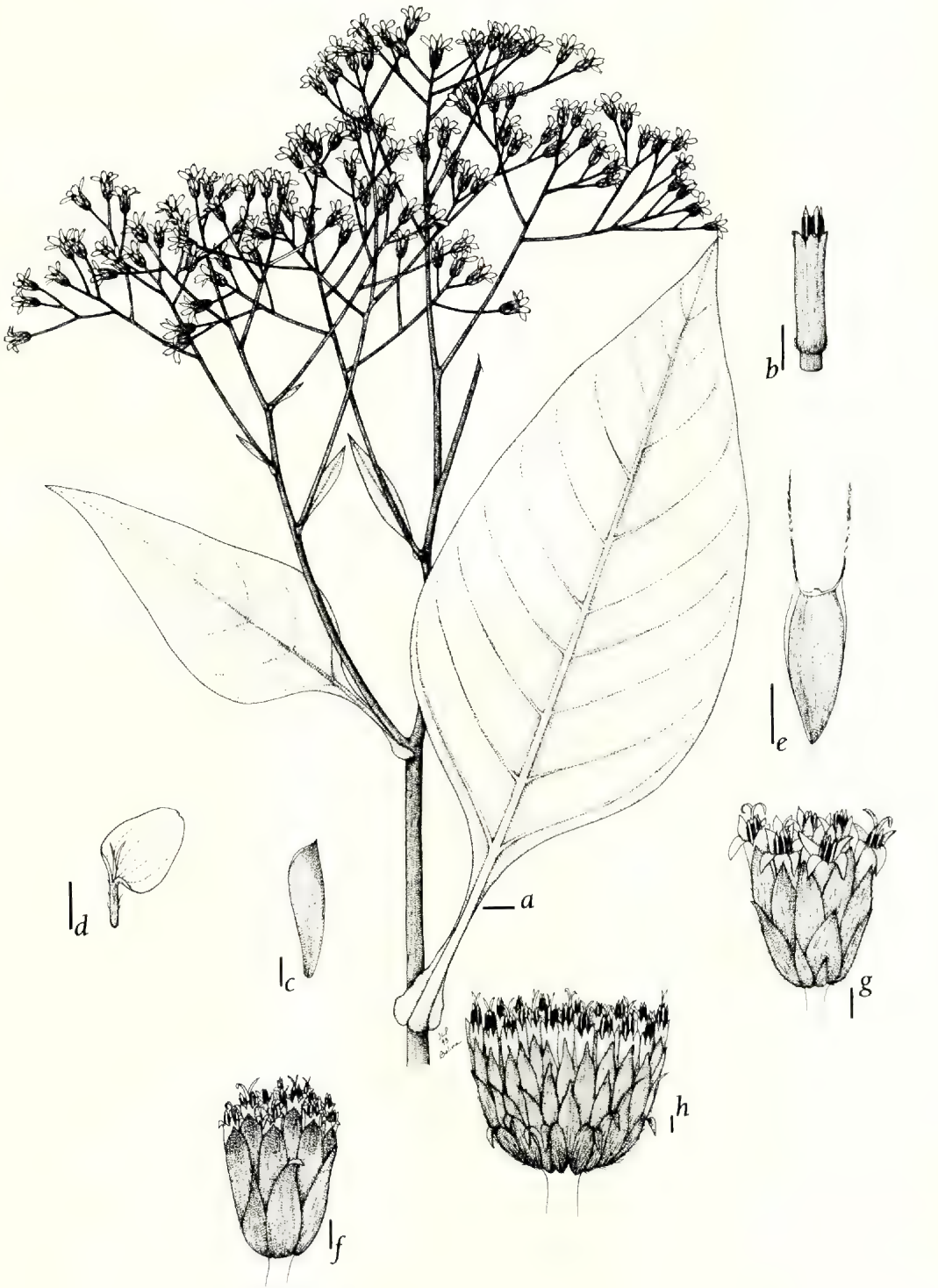

FIG. 6. *Verbesina lapazii*, *V. leucactinota*, and *V. semidecurrens*. a–f. *Verbesina lapazii* (*Beck 17629*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Head (ligules not shown). g. *Verbesina leucactinota* (*Bang 2135*). g. Head (ligules not shown). h. *Verbesina semidecurrens* (*García 608*). h. Head (ligules not shown). (a, bar = 1 cm; b–h, bar = 1 mm.)

Verbesina papasquiara Panero & Villaseñor, sp. nov.—TYPE: MEXICO. Durango: 93 km NW of Canatlán on rd to Santiago Papasquiaro, growing in disturbed *Pinus cembroides–Juniperus–Quercus* forest, 2170 m, 31 Aug 1991, *Panero, González & Acevedo 2264* (holotype: MEXU!; isotypes: CIIDIR! MICH! TENN! TEX! UC! US!). Fig. 5.

A *V. synoti* capitulis majoribus, floribus disci numerosioribus, et foliis basi non auriculatis differt.

Perennial herbs 1–1.5 m tall; stems terete, glabrescent, purplish green. Leaves opposite, triplinerved; blades 3–13 cm long, 1–8 cm wide, smaller distally towards the capitulescence, ovate to deltate, adaxial surface sparsely strigose, green, abaxial surface sparsely velutinous, pubescence denser along veins, slightly paler than adaxial surface, margins serrate to dentate, apex acuminate to acute, base truncate to attenuate and cuneately narrowed into the petiole; petioles 2–5 cm long, winged along distal 4/5 of petiole, rarely entirely winged, sometimes with small auricles at base. Capitulescence of 15–50+ heads, monochasial-thyrsoid; peduncles 1–4.5 cm long, moderately puberulent to strigose, purplish green. Heads radiate, campanulate, 1.2 cm high, 7–9 mm wide (excluding ligules); receptacle 1–2 mm wide, slightly convex. Phyllaries 11–13 in two subequal series; phyllaries of first series 4.5–6 mm long, 1–2 mm wide, spatulate, spreading, basal third indurate, puberulent, yellowish green, distal two-thirds herbaceous, puberulent, green; phyllaries of second series 4.5–6.5 mm long, 1–2 mm wide, lanceolate, appressed, basal two-thirds indurate, puberulent, yellowish green, distal third herbaceous, puberulent, green. Pales 8–8.5 mm long, 2.3–2.6 mm wide, lanceolate, conduplicate, keeled, chartaceous, protruding 1.5–3 mm beyond phyllaries, stramineous, apex acute, erect. Ray flowers 5–6, pistillate; corollas yellow-orange; tube 2 mm long, sparsely puberulent; ligule 8–9 mm long, 4.5–5.5 mm wide, oval, spreading, glabrous, apex rounded, trifid. Ray achenes 6–6.5 mm long, 3–3.5 mm wide (including wings), narrowly obovate, glabrous, stramineous-green; pappus of two awns 3 mm long. Disk flowers 18–25, corollas protruding 1–3 mm beyond pales; corollas yellow-orange, campanulate; tube 1.5 mm long, stramineous-yellow, sparsely puberulent; throat 4.8–5.3 mm long, 1 mm wide at base, 1.5 mm wide distally, sparsely puberulent; lobes 0.7–1 mm long, deltate, sparsely puberulent abaxially; anthers 2.5 mm long, thecae black, appendages 0.5 mm long, orange, ovate; styles 7 mm long; style branches ca 2 mm long. Disk achenes 7–7.5 mm long, 5–5.5 mm wide (including wings), obovate, glabrous, black, wings stramineous-green; pappus of two awns 2.5–3 mm long. Chromosome number: $n = 17$.

ADDITIONAL SPECIMEN EXAMINED. **Mexico.** DURANGO: Hwy 39, 20 km SE of Santiago Papasquiaro, 2 Aug 1970, *Flyr 1520* (TEX).

Verbesina papasquiara is known only from collections gathered at the first mountain range of the eastern side of the Sierra Madre Occidental. The low hills of this range are covered with disturbed *Pinus cembroides–Juniperus–Quercus* forest. *Verbesina papasquiara* is abundant along an intermittent creek on the west facing slopes of these mountains.

Verbesina papasquiara shares with *V. synotis* a similar yellow-orange corolla, leaf shape, and opposite leaves. It can be easily separated from this species by its larger heads and purplish green stems (for more distinguishing characteristics, see key under *V. hygrophila).*

Verbesina reyesii Panero & Villaseñor, sp. nov.—TYPE: MEXICO. Oaxaca: Distrito de Teposcolula, Anama, 3 km SE de San Vicente Nuñu, 2500 m, 25 Oct 1990, *Reyes 2683* (holotype: MEXU!; isotype: MICH!). Fig. 7.

A *V. hypoglauca* inflorescentiis minoribus, capitulis majoribus, et pappo nullo differt.

Small shrubs up to 1 m tall; stems terete, herbaceous parts puberulent, greenish white, woody parts glabrous, light brown. Leaves opposite with pinnate venation; blades 8–12.5 cm long, 3.5–5 cm wide, somewhat smaller distally towards the capitulescence, ovate to elliptical, adaxial surface sparsely hirsute to strigose, dark green, abaxial surface moderately sericeous, creamy green, veins conspicuously outlined against greenish background, sessile glandular trichomes sparsely distributed on abaxial surface, margins subentire to entire with 10–15 mucros at each side of the blade, apex acuminate, base rounded to attenuate; petiole 0.6–1 cm long. Capitulescence of 3 heads arranged in a simple dichasium; peduncles 6–9 cm long, puberulent, greenish white. Heads heterogamous, radiate, hemispheric, 1 cm high, 0.8–1 cm wide (excluding ligules); receptacle 5 mm wide, flat to slightly convex. Phyllaries 17–23 in 2–3 graduated series; phyllaries of first series 7–8 mm long, 2–2.5 mm wide, reflexed, herbaceous, foliaceous, lanceolate to oblong, pubescence like that of the leaves, green with reticulate venation, margins ciliate and slightly involuted; phyllaries of second and third series 4.5–5 mm long, 1 mm wide, appressed, herbaceous, chartaceous, oblong to lanceolate, resembling pales, sparsely puberulent, stramineous, greenish black at distal end, margins sparsely ciliate or glabrous. Pales 4.5 mm long, 0.5–0.7 mm wide, narrowly lanceolate, conduplicate, sparsely puberulent, stramineous, greenish black at distal end, apex acute. Ray flowers 7–10, corollas golden-yellow, pistillate; ligule, 1–1.2 mm long, 3.5 mm wide, oblong, moderately puberulent abaxially, veins on abaxial surface greenish black, apex conspicuously bifid; tube 1.3 mm long, sparsely puberulent. Ray achene 1.2–1.5 mm long (immature), oblong, glabrous, epappose. Disk flowers 50–70, corollas golden-yellow, hermaphrodite; throat 2 mm long, campanulate, sparsely puberulent; tube 1 mm long, moderately puberulent, greenish; lobes 0.6 mm long, sparsely puberulent on abaxial surface, yellow suffused with black especially at distal end; anthers 1.6 mm long, black, appendages 0.4 mm long, black; style 4 mm long, style branches 1.2 mm long, acute. Disk achene, 1.5 mm long (immature), oblanceolate, glabrous. Chromosome number unknown.

Verbesina reyesii shares with *V. sororia* A. Gray and *V. hypoglauca* Sch.-Bip. ex Klatt several morphological features. The three species have opposite, elliptical to ovate leaves with serrulate to entire margins and short petioles. In addition, they have sparsely to densely sericeous abaxial leaf surfaces, which give these species their characteristic light green to white abaxial leaf color. *Verbesina reyesii* can be readily distinguished from these two species by features of the involucre and capitulescence. In *V. reyesii* the involucre is graduated, and the phyllaries of the outermost series are foliose, reflexed, and exceed those of the innermost series; in *V. sororia* the involucre is not graduated, and the phyllaries of the outermost series do not exceed the innermost ones. Populations of *V. hypoglauca* from Oaxaca have involucres somewhat similar to those of *V. reyesii* in which the phyllaries of the outermost series are reflexed and longer than those of the innermost series. The phyllaries of these populations, however, are always smaller, and

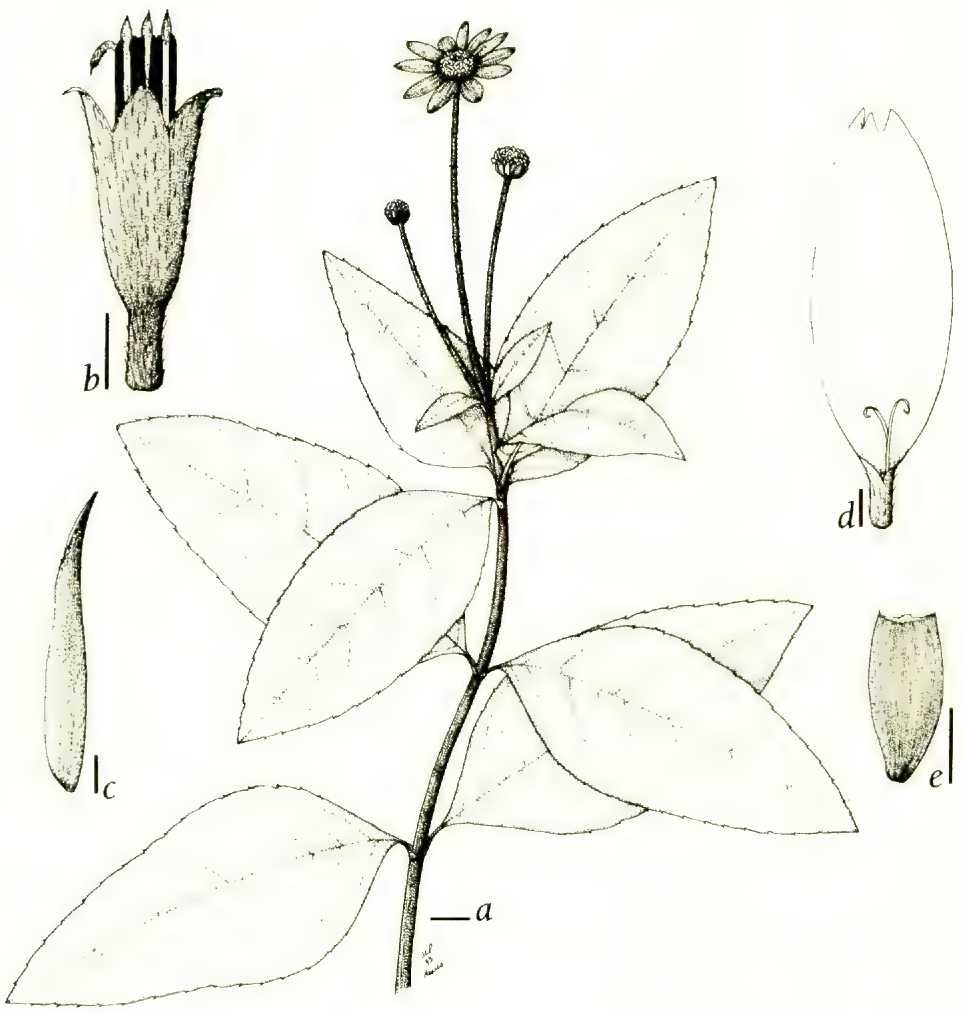

FIG. 7. *Verbesina reyesii* (*Reyes 2683*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. (a, bar = 1 cm; b–e, bar = 1 mm.)

not as reflexed and foliose as in *V. reyesii*. *Verbesina reyesii* can be further distinguished from the other two species by its capitulescence, which is a simple dichasium, whereas in *V. sororia* and *V. hypoglauca* the capitulescence is dichasial-thyrsoid with 12 to 50 heads. The achenes of *V. reyesii* are epappose, but pappose in *V. sororia* and *V. hypoglauca*.

The species epithet honors its collector, Jerónimo Reyes, a student at the Jardín Botánico, U.N.A.M., investigating the biogeographical and floristic affinities of the Flora of northwestern Oaxaca.

Verbesina strotheri Panero & Villaseñor, sp. nov.—TYPE: MEXICO. Chiapas: Mts WSW of San Cristóbal de Las Casas, along trail to San Lucas, approximately 200 m W of sewage tunnel entrance, 2100 m, *Panero & Salinas 2526* (holotype: MEXU!; isotypes: CAS! COL! ENCB! K! MA! MEXU! MICH! MY! QCA! RSA! SI! TENN! TEX! UC! US!). Fig. 8.

A *V. klattii* capitulis minoribus, floribus radii discique paucioribus, phyllariis majoribus, et foliis minoribus differt.

Shrubs 1–3 m tall; stems terete, herbaceous parts puberulent, purplish green, woody parts glabrous and brown-canescent. Leaves opposite, triplinerved; petiole 1.5–6 cm long, slightly canaliculate, winged along distal 2/3; blades 4.5–13 cm long, 2.5–10 cm wide, slightly smaller distally towards the capitulescence, ovate to broadly ovate, some leaves shallowly palmate, adaxial surface sparsely to moderately strigose, pale green, abaxial surface sparsely to moderately hirsute, stramineous pubescence denser on veins, effectively outlining them against green background, margins serrate to double-serrate, apex acuminate to acute, base truncate to obtuse and attenuate along petiole. Capitulescence of 3–25 heads, of simple dichasia or dichasial-thyrsoid; peduncles 0.5–5 cm long, moderately to densely puberulent, grayish purple. Heads heterogamous, radiate, hemispheric to campanulate, 1.2–2 cm high, 0.8–1.4 cm wide (excluding ligules); receptacle 0.5–0.8 cm wide, flat to slightly convex. Phyllaries 21–27 in 3–4 subequal series; phyllaries of first and second series 1–1.5 cm long, 0.8–1.2 cm wide, spreading, herbaceous, foliiform, somewhat bullate, suborbicular, light green drying dark green or black, sparsely puberulent; phyllaries of second and third series 1–1.2 cm long, 0.4–0.6 mm wide, appressed, chartaceous to scarious, lanceolate, sparsely puberulent or glabrous, distal half dark green drying black, margins glabrous. Pales 0.9–1.2 cm long, 0.25–0.35 mm wide, lanceolate, conduplicate, glabrous, stramineous, distal half dark green or blackish green, apex acute to acuminate. Ray flowers 5–7, corollas pale yellow, pistillate; ligules 1–1.5 cm long, 0.6–0.7 cm wide, ovate to elliptical, sparsely puberulent on veins of abaxial surface, apex trifid; tube 3 mm long, essentially glabrous. Ray achene 5 mm long, 3 mm wide including wings, flat to slightly biconvex, sometimes 3-angled, glabrous, grayish stramineous, pappus of two minute awns 0.3–0.5 mm long. Disk flowers 35–55, corollas pale yellow, hermaphrodite; throat 5 mm long, tubular to narrowly campanulate, sparsely puberulent; tube 3.5 mm long, glabrous; lobes 1 mm long; anthers 3.0–3.3 mm long, black, appendages 0.5 mm long, black; styles 7–8 mm long, style branches 1.5–2 mm long, acute. Disk achenes resembling ray achenes, 6–8 mm long, 4.5–5 mm wide, pappus like that of ray achene. Chromosome number: $n = 17$.

Additional Specimens Examined. **Mexico.** Chiapas: Around San Juan Chamula, 4 Nov 1987, *Santíz Ruíz 323* (CAS); Salida Tunel, 4–7 km W of San Cristóbal de Las Casas, 2100 m, 16 Oct 1980, *Breedlove & Strother 46337* (CAS), *46352* (CAS), 28 Oct 1981, *Breedlove 56000* (CAS).

Verbesina strotheri has only been collected from the low mountains surrounding the city of San Cristóbal de Las Casas. The area is dominated by moist oak and pine-oak forests with a well-developed shrub stratum. Interestingly, *V. strotheri* occurs only on the northern slopes of one of these hills and around the town of Chamula. The survival of this species is doubtful because of population pressures that are already evident at the base of these mountains.

Verbesina strotheri with its broad suborbicular phyllaries, opposite leaves, and light yellow corollas clearly belongs in section *Alatipes*, as outlined by Robinson and Greenman (1899). This species represents the southernmost extension of the group and the only member of the section in Chiapas. *Verbesina strotheri* is remarkable within the section because of its large suborbicular phyllaries and small number of ray flowers. It shares with *V. klattii* B. L. Rob. & Greenm. of western Mexico light yellow corollas and a somewhat similar phyllary morphology, although the heads of *V. klattii* are much larger and hemispherical. In addition, *Verbesina strotheri* has wingless stems, whereas *V. klattii* has winged stems.

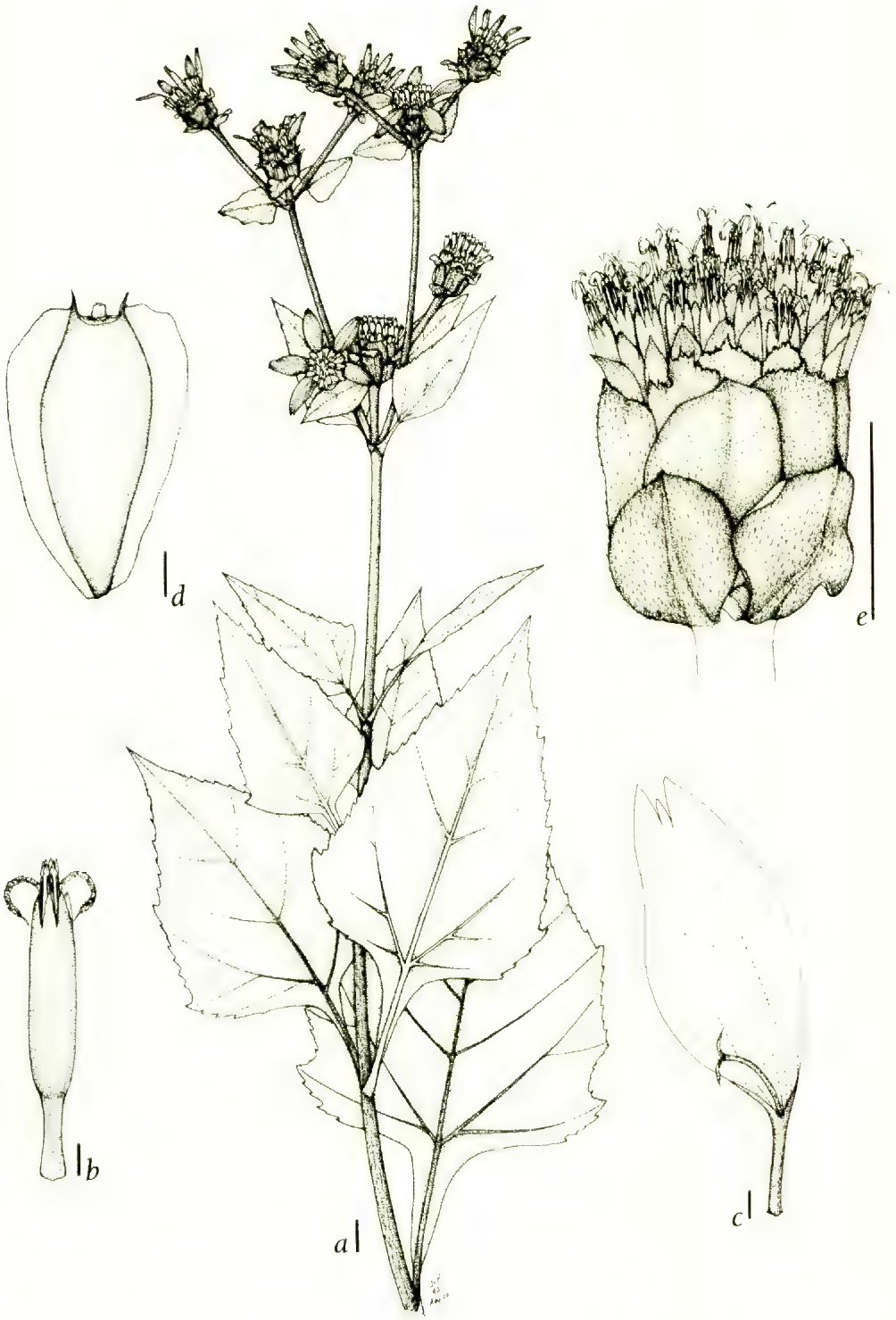

FIG. 8. *Verbesina strotheri* (*Panero & Salinas 2526*). a. Flowering branch. b. Disk corolla. c. Ray corolla. d. Disk achene. e. Head (ligules not shown). (a, e, bar = 1 cm; b–d, bar = 1 mm.)

The specific epithet honors John L. Strother, Curator of the Herbarium, University of California, Berkeley, who called to our attention this remarkable species.

Viguiera davilae Panero & Villaseñor, sp. nov.—TYPE: MEXICO. Puebla: Summit of Cerro Tepoxtla Grande (a peak of the Filo de La Tierra Colorada range) just NW of the village of San Martín de Esperilla and S of Chacnopalan, 2650 m, 1 Nov 1991, *Panero, Dávila & Tenorio 2581* (holotype: MEXU!; isotypes: ENCB! MEXU! MICH! TENN! TEX! UC! US!). Fig. 9.

A *V. bombycina* habitu stolonifero, phyllariis lanceolatis appressis, et acheniis pappo instructis differt.

Stoloniferous herbs becoming weak shrubs with age, 0.5–1.8 m tall; stems terete, herbaceous parts sparsely strigose to velutinous, greenish purple, woody parts glabrous, gray. Leaves opposite, triplinerved; blades 2.5–11 cm long, 0.8–3.8 cm wide, smaller distally towards the capitulescence, lanceolate, lowermost leaves trilobed, adaxial surface moderately to densely hirsute, grayish green, abaxial surface moderately to densely sericeous, bluish green, abaxial surface of lowermost leaves turning glabrous and pale green with age, margins entire to shallowly serrate, involute, apex acute to acuminate, base obtuse to attenuate along petiole; petiole 0.8–2 cm long. Capitulescence of 1–9 heads, simple monochasial cyme to monochasial-thyrsoid; peduncles 7–12 cm long, sparsely to moderately strigose to velutinous. Heads radiate, hemispherical, 1.2–1.5 cm high, 1.5–2.5 cm wide (excluding ligules); receptacle 0.8–1 cm wide, slightly convex. Phyllaries 28–35 in 3–4 subequal series, lanceolate; phyllaries of first series 8.8–9.2 mm long, 2.5–3 mm wide, appressed, base indurate, sparsely velutinous, dark green, herbaceous part moderately to densely velutinous, dark green, glabrous adaxially, margins ciliate; phyllaries of second, third, and fourth series 1–1.2 cm long, 3–3.5 mm wide, appressed, herbaceous, moderately to densely velutinous, dark green, margins ciliate. Pales 7.9–8.3 mm long, 3.3–3.6 mm wide, lanceolate, conduplicate, strongly keeled, chartaceous to somewhat coriaceous, barely protruding beyond phyllaries, basal half of pale glabrous, stramineous, distal half moderately velutinous, dark green or blackish green, apex acuminate erect. Ray flowers 11–16; corollas golden-yellow; tube 2 mm long, minutely puberulent; ligule 1.8–2.5 cm long, 5–8 mm wide, oblong, spreading, sparsely to moderately puberulent and glandular abaxially, veins black on abaxial surface, apex acute to rounded, bifid; ray ovaries 3.2–3.7 mm long, cuneate, triquetrous, sparsely puberulent, eppapose or with 1–3 squamellae, 0.3–0.5 mm long. Disk flowers 90–140, flowers protruding 2 mm beyond pales; corollas golden-yellow, narrowly campanulate; tube 1.3–1.6 mm long, moderately puberulent; throat 4.8–5.4 mm long, 1.3–1.5 mm wide, veins orange, sparsely to moderately puberulent; lobes 1.3–1.7 mm long, deltate, black on abaxial surface, moderately puberulent to tomentose abaxially; anthers 2.8–3.2 mm long, thecae black, appendages 0.6 mm long, broadly ovate to suborbicular, yellow-orange; styles 5.8–6.2 mm long, yellow-orange, style branches 2–2.4 mm long, tapered with a short appendage. Achenes, 3.5–4 mm long, 1.2–1.6 mm wide, biconvex, obovate, black, sparsely to moderately sericeous; pappus of 2 awns and 5–8 squamellae, awns 2.5–3 mm long, purplish stramineous, persistent, subequal, squamellae 0.4–0.7 mm long, free, same color as awns, persistent. Chromosome number unknown.

Viguiera davilae shares with *V. bombycina* S. F. Blake, *V. grammatoglossa* DC., *V. hidalgoana* E. E. Schill. & Panero, and *V. purpusii* Brandegee a similar

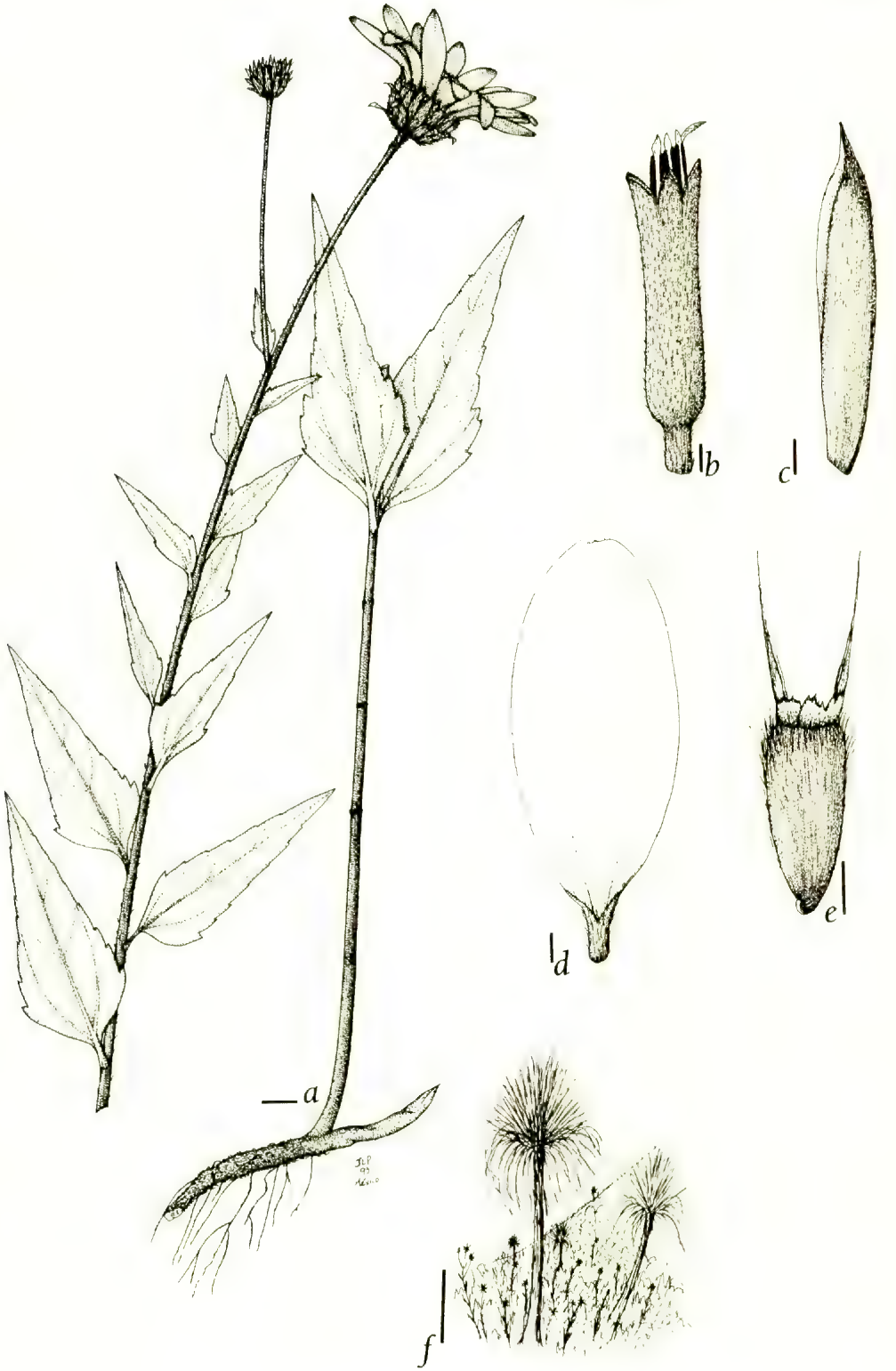

FIG. 9. *Viguiera davilae* (*Panero, Dávila & Tenorio 2581*). a. Flowering branch. b. Disk corolla. c. Pale. d. Ray corolla. e. Disk achene. f. Habit. (a, bar = 1 cm; b–e, bar = 1 mm; f, bar = 1 m.)

herbage pubescence, opposite leaves, a similar achene pappus morphology and color, and small capitulescences. *Viguiera davilae* can be readily distinguished from all these species by its lanceolate to trilobed leaves and the stoloniferous, herbaceous habit (unique, as far as known, among Mexican viguieras) that contrasts with the shrubby habit of the other species. Furthermore, *V. davilae* has appressed, lanceolate phyllaries, which are as long as or longer than the pales, a condition only observed in some populations of *V. grammatoglossa*.

Viguiera davilae appears to be a narrow endemic of the treeless gypsum hills of the Filo de La Tierra Colorada range north of Tehuacán. At the type locality, the species is abundant, growing in undisturbed oak shrubbery with *Perymenium mendezii* DC., *Tetrachyron brandegei* (Greenm.) Wussow & Urbatsch, *Tridax palmeri*, and *Nolina* sp.

The specific epithet honors our friend Patricia Dávila, chair of the Department of Botany, U.N.A.M.

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CAREX BRYSONII AND CAREX GODFREYI, NEW SPECIES OF CAREX SECTION GRISEAE (CYPERACEAE) FROM THE SOUTHEASTERN UNITED STATES

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The sedges constituting *Carex* section *Griseae* (L. H. Bailey) Kükenthal belong to subgenus *Carex* and possess glabrous leaf and bract blades, long-sheathing lower bracts, staminate terminal spikes, and glabrous perigynia with numerous (usually 40 or more) impressed nerves. Section *Griseae* [including sect. *Oligocarpae* (Carey) Mackenzie] contains 18 taxa, all endemic to eastern North America. The group is most diverse in the southeastern United States, the region inhabited by three of the section's four recently described species (Bryson et al. 1987; Kral et al. 1987; Bridges & Orzell 1989; Naczi 1989). The Southeast continues to yield new species of sect. *Griseae*; here I describe two new species from this area. Recognition of these taxa as new species results from ongoing research on the systematics of *Carex* sect. *Griseae* and exploration of localities and habitats in the Southeast with previously poorly known sedge floras.

Carex brysonii Naczi, sp. nov.—TYPE: USA. Alabama: Winston Co., [ca. 16 km (10 mi) N of Double Springs], Bankhead National Forest, Sipsey River Recreation Area, NE of Sipsey Fork, S of Winston Co. highway 60, T9S, R8W, Sect. 8, 15 May 1992, *Bryson 11610* (holotype: MICH!; isotypes: BM! BRIT/SMU! CAN! F! GA! GH! IBE! MO! NCU! NY! PH! TAES! TENN! UNA! US! VDB! VSC! WARM! ctb!). Figs. 1a, c, e, 2a, b.

Herba perennis, dense caespitosa. Rhizomata brevia, 0.2–1.0 mm longa inter surculos vel ramos rhizomatum, internodiis 0.2–1.0 mm longis, 2.4–2.7 mm crassis. Bases surculorum stramineae vel cinnamomeae. Culmi fertiles 26–63 cm alti, 0.5–0.8 mm lati in medio, sparsim antrorse scaberuli vel laeves. Folia 3–5; laminae 3.3–24 cm longae, 2.4–5.3 (–5.8) mm latae, lamina latissima (3.4–) 3.7–5.3 (–5.8) mm lata, glaucescentes, paginis abaxialibus laevibus vel papillatis; vaginae scabrae. Surculi vegetativi 8.7–56 cm alti; pseudoculmi 4.1–19 cm alti. Inflorescentiae 6.4–54 cm longae; spicae separatae vel 2–4 superae imbricatae; spicae infimae remotae. Spicae (3–) 4–5 (–6), erectae; spica terminalis (1.2–) 1.8–4.6 cm longa, 1.4–2.6 mm lata, omnino mascula, in pedunculo erecto 6.6–29 (–42) mm longo portata, spicas superas laterales vix vel multo superans; spica infima 0.9–2.8 cm longa, 3.8–4.7 mm lata, omnino feminea vel raro androgyna, in pedunculo erecto (0.9–) 2.3–13.2 cm longo portata; spicae laterales 0.6–2.6 cm longae, 3.8–6.8 mm latae, omnino femineae vel raro androgynae, in pedunculis erectis 0.3–4.9 cm longis portatae; flores feminei spicarum lateralium (2–) 3–8 spiraliter imbricati, internodio inter flores infimos (2.6–) 4.5–7.3 (–9.3) mm longo. Squamae femineae (3.5–) 4.1–6.1 mm longae, 1.3–2.0 mm latae, aristatae; corpus (2.0–) 2.5–3.2 (–3.8) mm longum, late ovatum vel ovatum, integrimarginatum; arista (0.1–) 1.2–3.6 mm

longa. Perigynia (3.7–) 4.0–4.7 (–5.1) mm longa, 1.5–1.7 (–1.8) mm lata, (2.2–) 2.5–3.1plo longiora quam latiora, ascendentia, obtuse trigona, nervata, glabra, ellipsoidea vel anguste ellipsoidea vel obovoidea vel anguste obovoidea, in basim angustam subacutam gradatim contracta, in rostrum laeve plus minusve excurvatum integrum (0.5–) 0.6–1.0 longum abrupte contracta; nervi 49–58 impressi. Achenia (2.5–) 2.7–3.5 mm longa, 1.4–1.6 mm lata, late obovoidea-ellipsoidea vel obovoidea-ellipsoidea, in stipitem 0.3–0.5 (–0.6) mm longum abrupte contracta, arcte inclusa perigyniis; corpus 2.1–2.7 mm longum.

Perennial herb, densely caespitose. Rhizomes short, 0.2–1.0 mm long between shoots or branches of the rhizomes, with internodes 0.2–1.0 mm long, 2.4–2.7 mm thick, covered with cataphylls 2–3.5 mm long. Shoot bases not surrounded by bases of old leaves, stramineous to cinnamon. Fertile culms 26–63 cm tall, 0.5–0.8 mm wide at mid-height, trigonous, erect to spreading, elongating slightly in fruit, sparsely antrorsely scaberulous-angled or smooth. Cataphylls scabrous, stramineous to cinnamon, multicostate. Leaves 3–5, arising in basal 0.01–0.2 (–0.6) of fertile culms, the longest 0.3–0.5 times as long as fertile culms; blades 3.3–24 cm long, 2.4–5.3 (–5.8) mm wide, the widest (3.4–) 3.7–5.3 (–5.8) mm wide, glaucescent, flat to barely plicate, margins antrorsely scaberulous or smooth, adaxial surface smooth or sparsely antrorsely scaberulous on main veins, abaxial surface smooth or papillate, papillae especially on leaves produced during previous season; leaf sheaths 2.1–10.4 cm long, tight, scabrous, glaucescent with bases stramineous to cinnamon; adaxial face of sheaths with hyaline and glabrous or apically sparsely scabrous band, hyaline band with apex slightly concave to slightly convex; ligules 1.2–4.7 mm long, lingulate with apex obtuse. Vegetative shoots 8.7–56 cm tall, 0.65–1.2 times as tall as culms; leaves 3–6, similar to those of fertile culms except blades 1.0–46 cm long; pseudoculms 4.1–19 cm tall, 1.9–3.2 mm wide, 0.28–0.39 of vegetative shoot height. Inflorescences 6.4–54 cm long, 0.22–0.86 of culm height, with spikes separate or upper 2–4 spikes overlapping; the uppermost lateral spikes 1.5–3.4 cm distant; the lowest spikes separate, (2.2–) 6.6–26 cm distant; lowest bract blade 5.6–22.9 cm long, sheath 0.6–7.4 cm long, adaxial face of sheath with glabrous and hyaline band usually occupying full length of sheath, hyaline band with apex slightly convex and elongated 0.3–2.3 mm above sheath apex, sheath scabrous abaxially, ligule 0.7–3.4 mm long; bract blade of uppermost lateral spike (0.7–) 2.0–6.3 (–8.2) cm long and overlapping but not exceeding terminal spike, sheath 1.3–2.6 mm long and glabrous or sparsely scabrous abaxially; uppermost bract subtending terminal spike and scale-like, sheathless, body 3.9–5.0 mm long, awn 0–7.9 mm long. Spikes (3–) 4–5 (–6), simple, single at nodes, erect; terminal spike (1.2–) 1.8–4.6 cm long, the longest (2.5–) 3.0–4.6 cm long, 1.4–2.6 mm wide, entirely staminate, 13–116-flowered, on erect peduncle 6.6–29 (–42) mm long, barely to much exceeding upper lateral spikes; lowest spike 0.9–2.8 cm long, 3.8–4.7 mm wide, entirely pistillate and (2–) 3–6-flowered or rarely androgynous with 4–5 pistillate and 1–3 staminate flowers, the flowers spirally imbricate, the internode between the lowest flowers (2.6–) 4.5–7.3 (–9.3) mm long, on erect peduncle (0.9–) 2.3–13.2 cm long; lateral spikes 0.6–2.6 cm long, 3.8–6.8 mm wide, entirely pistillate and (2–) 4–8-flowered or rarely androgynous with 3–8 pistillate and 1–7 staminate flowers, on erect peduncles 0.3–4.9 cm long. Staminate scales 3.8–4.3 mm long, 1.3–1.6 mm wide, narrowly oblong-obovate to oblong-obovate, obtuse to acute, awnless, center green and 1-nerved, margins hyaline and whitish to pale stramineous. Pistillate scales (3.5–) 4.1–6.1 mm long, 1.3–2.0 mm wide; body (2.0–) 2.5–3.2 (–3.8) mm long, broadly ovate to ovate with midrib prolonged

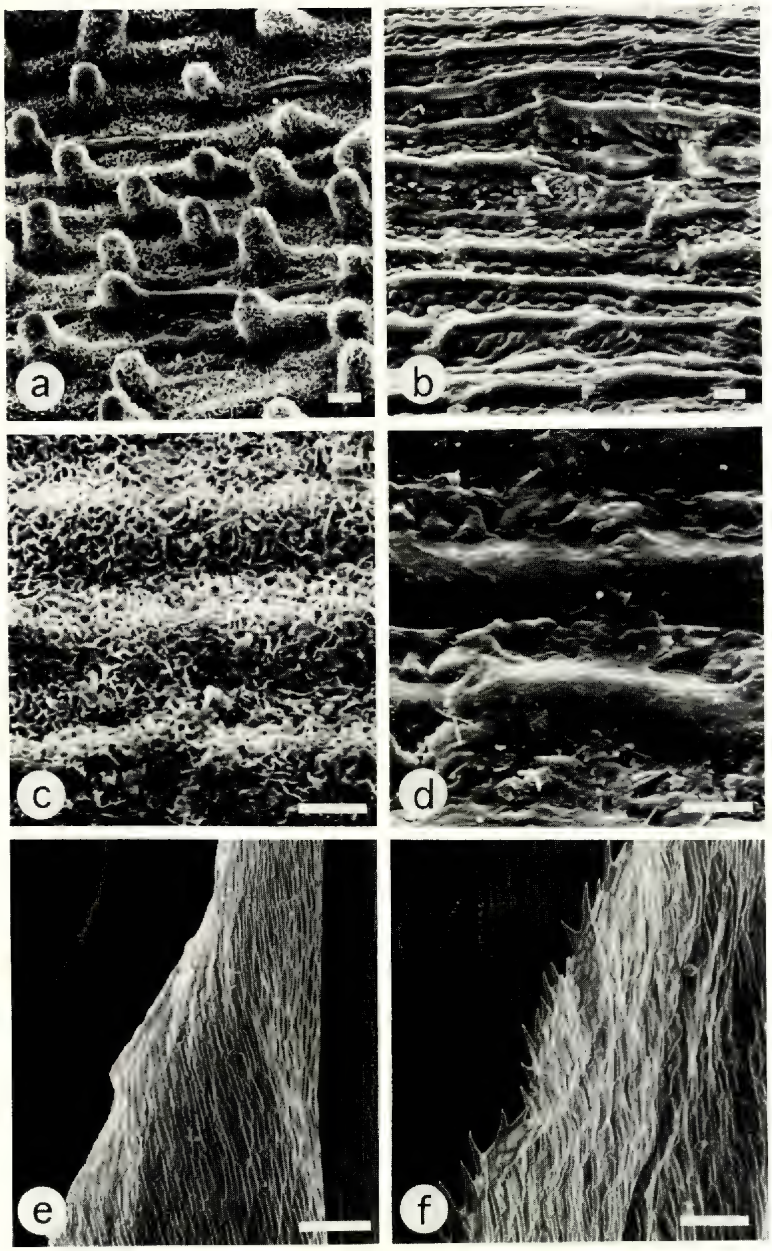

FIG. 1. Scanning electron micrographs of leaf surfaces and pistillate scale margins of *Carex brysonii* and *C. hitchcockiana*. a–b, abaxial surfaces of overwintered leaves: a. *C. brysonii* (*Bryson 4385*). b. *C. hitchcockiana* (*Naczi 1945*). c–d, adaxial surfaces of overwintered leaves: c. *C. brysonii* (*Bryson 4385*). d. *C. hitchcockiana* (*Naczi 1945*). e–f, margins of pistillate scale bodies, near apex of body: e. *C. brysonii* (*Naczi 2874*). f. *C. hitchcockiana* (*Naczi 1945*). Scale: bars in a–d = 0.01 mm; bars in e–f = 0.1 mm.

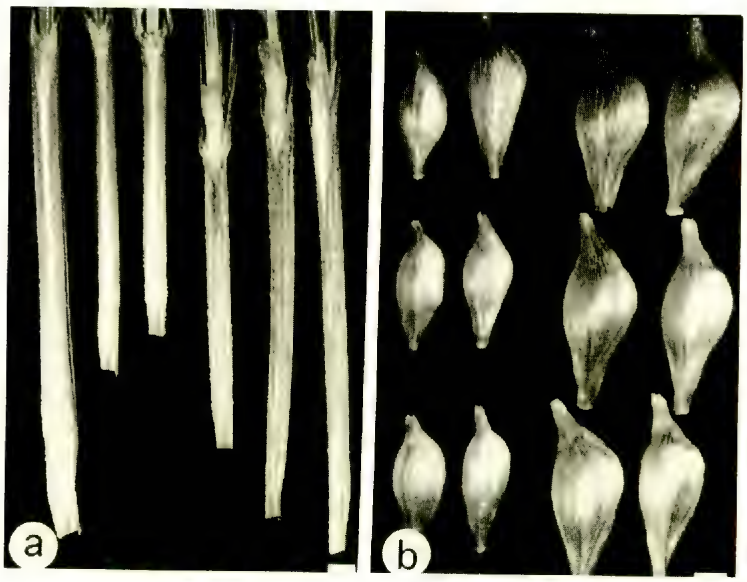

FIG. 2. Bract sheaths and perigynia of *Carex brysonii* and *C. hitchcockiana*. a, adaxial face of lowest bract sheath: left three sheaths *C. brysonii* (*Naczi 2874*), right three sheaths *C. hitchcockiana* (*Naczi 2546*). b, side view of perigynia: left two columns *C. brysonii* (*Bryson 4385*), right two columns *C. hitchcockiana* (*Naczi 2546*). Scale bars = 1 mm.

as antrorsely scaberulous awn (0.1–) 1.2–3.6 mm long, center green and 1–3-nerved, margins entire, hyaline, whitish. Anthers 3, 2.9–3.4 mm long. Styles jointed with achenes, withering; stigmas 3, 2.4–3.3 mm long. Perigynia (3.7–) 4.0–4.7 (–5.1) mm long, 1.5–1.7 (–1.8) mm wide, (2.2–) 2.5–3.1 times as long as wide, ascending, obtusely trigonous with faces flat to slightly convex, with many fine and deeply impressed nerves on each face, the total number of nerves 49–58, glabrous, green to red-brown, fusiform, ellipsoid or narrowly ellipsoid to obovoid or narrowly obovoid, gradually tapered to narrow and subacute base, abruptly contracted to beak; beak (0.5–) 0.6–1.0 mm long, 0.12–0.22 of perigynium length, smooth, slightly excurved, entire. Achenes (2.5–) 2.7–3.5 mm long, 1.4–1.6 mm wide, tightly enveloped by perigynia, broadly obovoid-ellipsoid to obovoid-ellipsoid, obtusely trigonous with faces slightly concave to flat, brown, basally abruptly contracted to stipe, apically abruptly contracted to beak; stipe 0.3–0.5 (–0.6) mm long, straight; body 2.1–2.7 mm long, 0.49–0.60 times as long as perigynium, with widest point 0.9–1.2 mm from body apex; beak 0.2 mm long, bent 30–70° from vertical.

Additional Specimens Examined. Alabama. Lawrence Co.: [ca. 19 km (11.6 mi) N of Double Springs], Bankhead National Forest, W side of Borden Creek, T8S, R8W, Sect. 32, *Bryson 11619* (MICH, US, VDB, ctb). Winston Co.: type locality, *Bryson 4385* (DOV, IBE, MICH, MO, NLU, PH, UNA, VDB, ctb), *Naczi 2874* (GH, MICH, NY, UNA, US, VDB, ctb); Bankhead National Forest, SE of Sipsey River Recreation Area, W side of river, [T9S, R8W], Sect. 10, *Bryson 2536* (MICH, ctb); Bankhead National Forest, SE by ca. 1 mi from Sipsey River Recreation Area, T9S, R8W, Sect. 9, *Bryson 4381* (BRIT/SMU, LSU, MICH, MO, MSC, NLU, PH, TAES, UARK, VDB, VSC, ctb).

TABLE 1. Morphologic characters distinguishing *Carex brysonii* from *C. hitchcockiana*.

	C. brysonii	*C. hitchcockiana*
leaf color	glaucescent	deep green
abaxial surface of overwintered leaves	usually papillate	smooth or sparsely scabrous on midrib
hyaline band of lowest bract sheath, length relative to sheath	usually as long as sheath	much shorter than sheath
bract blade of uppermost lateral spike, length relative to terminal spike	shorter than or equalling terminal spike	usually much exceeding terminal spike
longest terminal spike, length (mm)	(25–) 30–46	(3.4–) 14–34 (–42)
pistillate scale margins	entire	denticulate
perigynium, length (mm)	(3.7–) 4.0–4.7 (–5.1)	(4.5–) 4.6–5.6 (–6.2)
perigynium, width (mm)	1.5–1.7 (–1.8)	1.9–2.2 (–2.3)

Morphologically, *C. brysonii* is most similar to *C. hitchcockiana* Dewey. These two are the only taxa in sect. *Griseae* to have scabrous leaf and bract sheaths. In addition, *C. brysonii* and *C. hitchcockiana* share brown shoot bases, relatively wide leaves [the widest leaf blade per plant (3.0–) 3.5–5.3 (–6.5) mm wide], perigynia tightly enveloping the achenes, and perigynia with excurved beaks. Numerous morphologic characters distinguish the two species (Table 1). The abaxial surfaces of the leaf blades of *C. brysonii* are smooth or papillate. Leaves produced during the previous season (overwintered leaves) are most often papillate, whereas leaves produced early in the current season are usually smooth. Thus, only some of the leaves per specimen are papillate, but every specimen I have examined bears at least a few papillate leaves. The papillae, which are minute (barely visible with 10× magnification), densely cover the leaf surface (Fig. 1a). In contrast, the abaxial surfaces of the leaf blades of *C. hitchcockiana* are smooth or sparsely scabrous on the midribs (Fig. 1b). The leaf blades of *C. brysonii* bear a thin covering of wax, both abaxially (Fig. 1a) and adaxially (Fig 1c). This wax, which may be worn off old leaves, causes the leaves to be glaucescent. *Carex hitchcockiana* lacks this wax covering on both surfaces of its deep green leaves (Figs. 1b, d). In *C. brysonii*, the hyaline band of the lowest bract sheath usually occupies the full length of the sheath and is elongated above the sheath apex only 0.3–2.3 mm (Fig. 2a). *Carex hitchcockiana*, on the other hand, has the hyaline band of the lowest bract sheath confined to the upper portion of the sheath and elongated above the sheath apex (0.6–) 1.0–5.6 (–6.6) mm (Fig. 2a). The bract blade of the uppermost lateral spike overlaps but does not exceed the terminal spike in *C. brysonii*, but usually much exceeds it in *C. hitchcockiana*. In addition, the terminal spikes of *C. brysonii* are longer than those of *C. hitchcockiana*. The pistillate scale bodies of *C. brysonii* have entire margins (Fig. 1e), whereas those of *C. hitchcockiana* are denticulate (Fig. 1f). Furthermore, the perigynia of *C. brysonii* are shorter and narrower than the perigynia of *C. hitchcockiana* (Fig. 2b).

In size and shape, the perigynia of *C. brysonii* are almost identical to those of *C. asynchrona* Naczi. Many other characters differentiate these two species, though. Unlike *C. brysonii*, *C. asynchrona* possesses pale green leaf blades that lack papillae and are relatively narrow [the widest blade per plant only 2.5–4.0 mm wide versus (3.4–) 3.7–5.3 (–5.8) mm wide for *C. brysonii*], smooth leaf and bract sheaths,

relatively short terminal spikes [the longest spike per plant only 17–27 (–35) mm long versus (25–) 30–46 mm], and quite crowded upper spikes [only 0.7–1.5 (–2.2) cm between the uppermost lateral spikes versus 1.5–3.4 cm].

Carex brysonii grows in shaded, moist, sandy loam on slopes above streams in forests dominated by *Acer saccharum* Marsh., *Carpinus caroliniana* Walt., *Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L., *Magnolia macrophylla* Michx., *Pinus* sp., and *Tsuga canadensis* (L.) Carr. *Carex communis* L. H. Bailey, *C. oligocarpa* Willd., and *C. picta* Steud. associate closely with *C. brysonii*. I have seen only 6 collections of *C. brysonii*, despite examining specimens of sect. *Griseae* from over 60 herbaria. Apparently first collected in 1979 (*Bryson 2536*) and known only from along a short portion of the Sipsey Fork of the Black Warrior River and an immediately confluent portion of Borden Creek, *C. brysonii* appears to be a narrow endemic to gorges of the upper Sipsey Fork drainage. At least one other vascular plant taxon is endemic to these gorges, *Thelypteris pilosa* var. *alabamensis* Crawford (Norquist 1991). The upper Sipsey Fork drainage, in the Cumberland Plateau (Appalachian Plateaus) physiographic province, is also noteworthy for harboring the southernmost populations known of several species of *Carex* of eastern North American mesic forests: *C. careyana* Dewey, *C. gracillima* Schwein., *C. laxiflora* Lam. var. *laxiflora*, and *C. pedunculata* Willd. (Bryson 1980; Kral 1981; Naczi & Bryson 1990), but not "*C. hitchcockiana*" as noted by Naczi and Bryson (1990: 51), which is *C. brysonii*. Occurring farther south than *C. hitchcockiana*, *C. brysonii* is disjunct approximately 100 kilometers (60 miles) from the nearest known population of *C. hitchcockiana* [ALABAMA. Madison Co.: NE of Monte Sano Mt., between Monte Sano State Park and Hwy 72, *Bryson 2046* (FLAS, ctb)].

In appreciation for the many ways he has assisted me in my studies of *Carex*, I name this species for Dr. Charles T. Bryson, avid student of the genus, discoverer of the species, and friend. Charles's insistence that I see *C. brysonii* in the field induced me to visit what is now the type locality, carefully examine the plant, and consequently comprehend its uniqueness.

Carex godfreyi Naczi, sp. nov.—TYPE: U.S.A. Florida: Lake Co., Astor Park, 0.2 mi E of routes 40 & 445A junction, along N side of route 40, 22 Apr 1991, *Naczi 2781* (holotype: MICH!; isotypes: FLAS! FSU! NCU! NY! US! VDB! ctb!). Fig. 3a, b.

Herba perennis, dense vel laxe caespitosa. Rhizomata brevia vel longa, 0.2–38 mm longa inter surculos vel ramos rhizomatum, internodiis 0.2–12.4 mm longis, 1.2–2.0 mm crassis. Bases surculorum atrovinosae usque ad (3.4–) 4.0–7.3 cm. Culmi fertiles 7.8–65 (–85) cm alti, 0.4–0.9 mm lati in medio, laeves. Folia 2–4; laminae 1.4–34 cm longae, 1.1–4.0 (–5.3) mm latae, lamina latissima 2.4–4.0 (–5.3) mm lata, virides, paginis abaxialibus laevibus; vaginae glabrae. Surculi vegetativi 23–63 cm alti; pseudoculmi 3.3–12.9 cm alti. Inflorescentiae 3.8–58 cm longae; spicae 2–4 superae imbricatae; spicae infimae remotae. Spicae (3–) 4–5 (–6), erectae; spica terminalis 0.7–3.7 (–4.6) cm longa, 1.0–2.9 mm lata, omnino mascula, in pedunculo erecto 1.6–22 (–51) mm longo portata, spicas superas laterales vix superans; spica infima 0.5–1.9 cm longa, 4.6–7.0 mm lata, omnino feminea, in pedunculo erecto vel arcuato 2.9–13.3 (–18.1) cm longo portata; spicae laterales 0.7–2.6 cm longae, 4.6–9.2 mm latae, omnino femineae vel raro androgynae, in pedunculis erectis 0.1–4.9 cm longis portatae; flores feminei spicarum lateralium

3–19 spiraliter imbricati, internodio inter flores infimos 1.8–3.3 (–6.2) mm longo. Squamae femineae 2.1–5.3 mm longae, 1.2–2.4 mm latae, aristatae; corpus 1.7–2.8 mm longum, late ovatum vel ovatum, integrimarginatum; arista (0–) 0.2–3.3 mm longa. Perigynia (4.0–) 4.3–5.0 (–5.6) mm longa, 1.5–1.9 (–2.1) mm lata, 2.4–2.9 (–3.2)plo longiora quam latiora, ascendentia, obtuse trigona, nervata, glabra, ellipsoidea vel anguste ellipsoidea vel obovoidea vel anguste obovoidea, in basim latam truncatam gradatim contracta, in apicem subacutum rectum vel vix excurvatum gradatim contracta, erostrata vel rostro minuto laevi recto integro usque ad 0.2 mm longo instructa; nervi 52–64 impressi. Achenia (3.0–) 3.1–3.5 (–3.7) mm longa, 1.5–1.8 mm lata, late obovoidea vel obovoidea, in stipitem 0.6–0.8 (–0.9) mm longum abrupte contracta, laxe inclusa perigyniis; corpus 2.0–2.4 (–2.6) mm longum.

Perennial herb, densely to loosely caespitose. Rhizomes short to long, 0.2–38 mm long between shoots or branches of the rhizomes, with internodes 0.2–12.4 mm long, 1.2–2.0 mm thick, covered with cataphylls 2–15 mm long. Shoot bases not surrounded by bases of old leaves, dark purple-red to (3.4–) 4.0–7.3 cm high. Fertile culms 7.8–65 (–85) cm tall, 0.4–0.9 mm wide at mid-height, trigonous, erect to spreading, elongating in fruit, smooth. Cataphylls glabrous, red-brown to purple-red, multicostate. Leaves 2–4, arising in basal 0.01–0.3 of fertile culms, the longest 0.1–0.6 times as long as fertile culms; blades 1.4–34 cm long, 1.1–4.0 (–5.3) mm wide, the widest 2.4–4.0 (–5.3) mm wide, green, flat to barely plicate, margins antrorsely scaberulous, adaxial surface smooth or sparsely antrorsely scaberulous on main veins, abaxial surface smooth; leaf sheaths 3.1–9.2 cm long, loose, glabrous, green with bases tinged with purple-red; adaxial face of sheaths with hyaline and glabrous band, hyaline band with apex slightly concave or truncate; ligules 1.8–4.2 (–10.9) mm long, lingulate with apex obtuse or inverted V-shaped with apex acute. Vegetative shoots 23–63 cm tall, 0.6–1.5 times as tall as culms; leaves 4–7, similar to those of fertile culms except blades 5.7–48.5 cm long; pseudoculms 3.3–12.9 cm tall, 1.0–3.8 mm wide, 0.16–0.27 of vegetative shoot height. Inflorescences 3.8–58 cm long, 0.094–0.94 of culm height, with the upper 2–4 spikes overlapping; the uppermost lateral spikes 0.3–8.5 (–19.5) cm distant; the lowest spikes separate, 7.8–31 cm distant; lowest bract blade 8.8–34.4 cm long, sheath 1.1–6.9 cm long, adaxial face of sheath with glabrous and hyaline band occupying full length of sheath or confined to upper portion of sheath, hyaline band with apex slightly concave to slightly convex and elongated 0.1–0.6 (–1.1) mm above sheath apex, sheath glabrous abaxially, ligule 0.9–3.9 (–6.6) mm long; bract blade of uppermost lateral spike 0.6–7.5 (–12.4) cm long and slightly exceeding terminal spike or rarely much exceeding terminal spike, sheath 1.4–7.1 mm long and glabrous; uppermost bract subtending terminal spike and scalelike, sheathless, body 3.4–5.1 mm long, awn 0.8–4.9 mm long. Spikes (3–) 4–5 (–6), simple, single at nodes, erect; terminal spike 0.7–3.7 (–4.6) cm long, the longest 1.2–3.7 (–4.6) cm long, 1.0–2.9 mm wide, entirely staminate, 11–94-flowered, on erect peduncle 1.6–22 (–51) mm long, usually barely exceeding upper lateral spikes; lowest spike 0.5–1.9 cm long, 4.6–7.0 mm wide, entirely pistillate, 3–10-flowered, the flowers spirally imbricate, the internode between the lowest flowers 1.8–3.3 (–6.2) mm long, on erect or arched peduncle 2.9–13.3 (–18.1) cm long; lateral spikes 0.7–2.6 cm long, 4.6–9.2 mm wide, entirely pistillate and 4–19-flowered or rarely androgynous with 3–17 pistillate and 2–16 staminate flowers, on erect peduncles 0.1–4.9 cm long. Staminate scales 3.3–4.8 mm long, 1.1–1.6 mm wide, narrowly oblong to oblong or oblong-ovate, acute to acuminate, awnless, center green and 1-nerved,

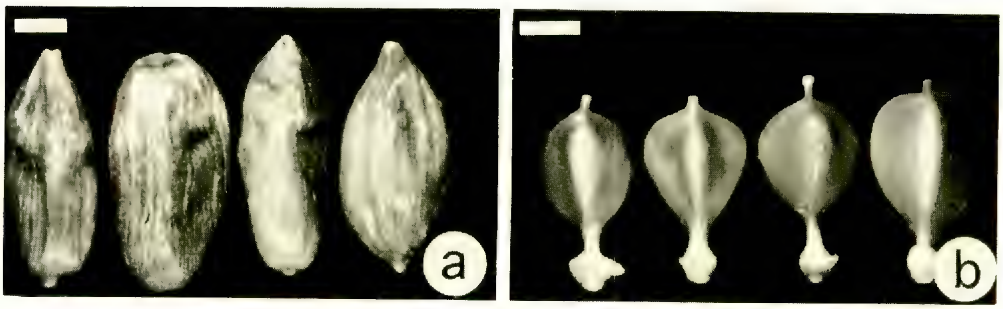

FIG. 3. Perigynia and achenes of members of the *Carex grisea* complex. a, front view of perigynia of (left to right) *C. amphibola* (*Naczi 2557*), *C. corrugata* (*Naczi 1033*), *C. godfreyi* (*Naczi 2376*), and *C. grisea* (*Naczi 1854*). b, front view of achenes (retaining portions of perigynium bases adnate to achene stipes) of (left to right) *C. amphibola* (*Naczi 2557*), *C. corrugata* (*Naczi 1033*), *C. godfreyi* (*Naczi 2376*), and *C. grisea* (*Naczi 1854*). Scale bars = 1 mm.

margins hyaline and whitish to stramineous or whitish with red-brown speckles. Pistillate scales 2.1–5.3 mm long, 1.2–2.4 mm wide; body 1.7–2.8 mm long, broadly ovate to ovate with midrib prolonged as antrorsely scaberulous awn (0–) 0.2–3.3 mm long, center green and 1–3-nerved, margins entire, hyaline, whitish and usually with red-brown speckles. Anthers 3, 2.0–2.8 mm long. Styles jointed with achenes, withering; stigmas 3, 1.8–2.7 mm long. Perigynia (4.0–) 4.3–5.0 (–5.6) mm long, 1.5–1.9 (–2.1) mm wide, 2.4–2.9 (–3.2) times as long as wide, ascending, obtusely trigonous with faces flat to slightly convex or rugose, with many fine and deeply impressed nerves on each face, the total number of nerves 52–64, glabrous, green to red-brown, ellipsoid or narrowly ellipsoid to obovoid or narrowly obovoid, very gradually tapered to broad and truncate base, gradually tapered to subacute and straight or slightly excurved apex, beakless or with minute beak; beaks 0–0.2 mm long, 0–0.03 of perigynium length, straight, entire. Achenes (3.0–) 3.1–3.5 (–3.7) mm long, 1.5–1.8 mm wide, loosely enveloped by perigynia, broadly obovoid to obovoid, obtusely trigonous with faces slightly concave to flat, brown, basally abruptly contracted to stipe, apically abruptly contracted to beak; stipe 0.6–0.8 (–0.9) mm long, straight; body 2.0–2.4 (–2.6) mm long, 0.43–0.53 times as long as perigynium, with widest point 0.7–1.1 (–1.2) mm from body apex; beak 0.3–0.6 mm long, usually vertical, but occasionally bent 10–30° from vertical.

Representative Specimens. Florida. Bay Co.: 1 mi N of Bennett, in bottoms of Moccasin Creek, *McDaniel 7378* (BRIT/SMU, FLAS, FSU, TENN, UNA, VDB, ctb). Citrus Co.: Chassahowitzka, along Chassahowitzka River just W of county park, *Naczi 2791* (MICH, ctb). Clay Co.: ca. 1 mi N of Green Cove Springs, Magnolia Springs, 0.4 mi N of rte. 17, *Naczi 2374* (MICH, ctb), *Naczi 2771* (MICH, ctb); Magnolia, 17 Mar 1883, *J. D. Smith s.n.* (NY, US). Columbia Co.: Ichetucknee Springs, *Godfrey 62661 & Houk* (FSU, NCU); 3 mi W of Lula, *McDaniel 6088* (NY, FLAS, FSU). Dixie Co.: ca. 1 mi N of Jena, near the Steinhatchee River, *Godfrey 74658* (FLAS, FSU, MO, NCU, VDB); ca. 2.5 mi NE of Jena, 2.6 mi SW of jct. of rtes. 358 & 98, SE of rte. 358, *Naczi 2376* (MICH, ctb), *Naczi 2796* (MICH, ctb). Duval Co.: near Jacksonville, *Curtiss 3267* (FLAS), *Curtiss 4682* (F, FSU, MO, NY, US); ca. 2 mi W of Bayard along W side of Julington Creek, S of Old St. Augustine Rd., *Naczi 2773* (MICH, ctb). Gadsden Co.: near River Junction, *Curtiss 6401* (BH, CU, DOV, GH, ILL, MIN, MO, NY, US, WARM); near Chattahoochee, E side of Florida State Hospital Pond, *Gholson 9655 & Cameron* (FLAS, FSU). Hillsborough Co.: Hillsborough River State Park, *Bright 456* (FLAS, PH), *Bright 457* (CM), *Lakela 25693 & R. W. Long* (BRIT/SMU, FLAS, OKLA, USF). Jackson Co.: near Marianna, Florida Caverns State Park, *Gholson 9606* (FSU), *Godfrey 53180* (DUKE, FSU, GH); W of Malone, along Cowarts Creek, *Godfrey 74825* (FSU); ca. 1 mi N of Marianna, N of rte. 167 along W side of Chipola River, *Naczi 2106* (MICH, ctb). Jefferson Co.:

Wacissa Springs, *Godfrey 53492* (DUKE, FSU, GH), *Godfrey 60798* (FSU), *Godfrey 60800* (NY), *Godfrey 74806* (FSU, VDB); E of Newport, 1 mi W of Aucilla River, by rte. 98, *Godfrey 75769* (FSU); E of Newport, 0.4 mi W of Aucilla River, by rte. 98, *Bryson 7920* (MICH, ctb), *Gholson 11299* (FLAS, ctb), *Godfrey 81821 & Gholson* (FSU), *Godfrey 82028 & Naczi* (FLAS, FSU), *McNeilus 90-125* (WARM), *Naczi 1109 & Godfrey* (FSU, MICH, ctb), *Naczi 2098* (FLAS, FSU, MICH, US, VSC, ctb). Leon Co.: near Horne Springs, between springs and St. Marks River, *Godfrey 82007* (FLAS, FSU, VDB); ca. 0.5 mi S of Ochlockonee, *Harper 14* (BH, ILL, NY, US); ca. 1 mi W of Bloxham, E side of Ochlockonee River just S of rte. 20, *Naczi 2100* (MICH). Levy Co.: 2 mi S of Otter Creek, *Godfrey 74739* (FLAS, FSU); just E of Rosewood, 15 mi E of Cedar Key, *Kral 57328* (VDB). Liberty Co.: 8 mi E of Hosford, *McDaniel 5913* (FSU). Marion Co.: E of Silver Springs, *Orzell & Bridges 13296* (MICH). Martin Co.: Stuart and vicinity, Jan–Feb 1917, *Atwood s.n.* (CU). Nassau Co.: 1.8 mi N of Callahan along W side of rte. 1, *Naczi 2370* (FLAS, FSU, MICH, ctb), *Naczi 2371* (FLAS, FSU, MICH, VDB, VSC, ctb). Pasco Co.: E of Land o' Lakes, Cypress Creek Wellfield, *Crewz 1563* (UNA, USF), 9 Apr 1979, *T. F. Rochow s.n.* (USF). St. Johns Co.: ca. 3 mi SE of Orangedale, S of rte. 16 along E side of Trout Creek, *Naczi 2778* (FLAS, FSU, MICH, VDB, VSC, ctb). Taylor Co.: rte. 98/19/27A at Steinhatchee River, *Gholson 6077 & Godfrey* (FLAS); ca. 5.5 mi W of Hampton Springs along N side of rte. 98, *Naczi 2382* (MICH). Wakulla Co.: along the Wakulla River at Upper Bridge, *Godfrey 53090* (FSU, GA, GH, NY, USF, VDB); vicinity of St. Marks, *Godfrey 60666* (FSU), *Godfrey 60668* (FSU, GH, NY); Newport, along the St. Marks River, *Godfrey 61744* (FSU), *Godfrey 63258* (FLAS, FSU, LL, NCU, US, USF); bottoms of St. Marks River near north edge of county, *Harper 60* (GH, MIN, NY); ca. 0.7 mi N of Newport, just S of Newport Spring, *Naczi 2384* (FLAS, FSU, MICH, ctb). Washington Co.: N edge of Vernon, above Holmes Creek under hwy. 79 bridge, *Anderson 12629* (FSU, MICH).—GEORGIA. Calhoun Co.: 3 mi W of Leary, near Ichawaynochaway Creek, *Thorne 7995 & Muenscher* (CU, GA). Early Co.: 4 mi E of Blakely, along Dry Creek, *Thorne 2948, Muenscher, & S. J. Smith* (CU, GA, GEO, GH). Lee Co.: near Armena, along Fowltown Creek, *Thorne 9025 & Muenscher* (CU, GEO).—NORTH CAROLINA. Jones Co.: 5 mi NE of Pollocksville, bank of Island Creek near co. rd. 1004, *Sears C179* (NLU). New Hanover Co.: Wilmington, Delgado, *Churchill 132* (GH).—SOUTH CAROLINA. Allendale Co.: Savannah River Operations Area of Atomic Energy Commission, 6 May 1952, *Batson & Kelley s.n.* (USCH).

Carex godfreyi belongs to a complex of four species, including *C. amphibola* Steud., *C. corrugata* Fern., and *C. grisea* Wahlenb. The characters that define the *C. grisea* complex are purple-red shoot bases (rarely brown in *C. amphibola* and *C. grisea*), loose leaf and bract sheaths, perigynia loosely enveloping the achenes, perigynia relatively long [(3.6–) 3.9–5.3 (–5.6) mm long], and perigynium length/achene body length ratio relatively high [(1.7–) 2.0–2.4 (–2.6)]. *Carex godfreyi* differs from all the other members of the *C. grisea* complex in several ways (Table 2). First, it is the only member of the complex that is loosely caespitose. Second, the purple-red coloration of the leaf sheaths and cataphylls extends higher from the shoot bases in *C. godfreyi* than in the three other species. Third, the leaf blades of *C. godfreyi* are narrower than those of the others. Finally, *C. godfreyi* has the longest achene stipes of any member of the complex (Fig. 3b). Within the *C. grisea* complex, *C. godfreyi* is morphologically most similar to *C. amphibola*. Both species possess relatively narrow perigynia with relatively high length/width ratios (Table 2, Fig. 3a).

Carex godfreyi inhabits wet hammocks, swamps, and floodplains dominated by deciduous trees. It grows in shaded, wet, calcareous mucks or sandy loams, often with *Acer rubrum* L., *Asclepias perennis* Walt., *Carex bromoides* Willd., *C. leptalea* Wahlenb., *Carpinus caroliniana*, *Platanthera flava* (L.) Lindl., *Rhapidophyllum hystrix* (Pursh) Wendl. & Drude, *Rhynchospora miliacea* (Lam.) Gray, *Ruellia caroliniensis* (Gmel.) Steud., *Sabal minor* (Jacq.) Pers., *S. palmetto* Schult. & Schult., and *Samolus parviflorus* Raf. *Carex godfreyi* occurs on the Coastal Plain from southeastern North Carolina south to central peninsular Florida and west to southwestern Georgia and nearby portions of the panhandle of Florida.

TABLE 2. Morphologic characters distinguishing *Carex godreyi* from the rest of the members of the *Carex grisea* complex.

	C. godfreyi	*C. amphibola*	*C. corrugata*	*C. grisea*
habit	densely to loosely caespitose	densely caespitose	densely caespitose	densely caespitose
purple-red coloration at plant base, height (mm)	(34–) 40–73	(0–) 10–24	(4–) 13–36 (–39)	0–32
widest leaf per plant, width (mm)	2.4–4.0 (–5.3)	4.4–6.8	3.3–5.6 (–8.0)	(4.8–) 5.0–6.8 (–9.1)
perigynium, width (mm)	1.5–1.9 (–2.1)	1.5–1.9 (–2.2)	(1.7–) 1.8–2.3 (–2.4)	(1.8–) 2.0–2.6
perigynium, length/width	2.4–2.9 (–3.2)	(2.2–) 2.5–3.1	1.8–2.3 (–2.5)	1.8–2.4 (–2.6)
achene stipe, length (mm)	0.6–0.8 (–0.9)	(0.3–) 0.4–0.6	(0.3–) 0.4–0.6	(0.2–) 0.3–0.4 (–0.5)

The populations of *C. godfreyi* are relatively few and often widely discontinuous, presumably due to the species' requirement for a specialized habitat. Only two collections are known from North Carolina, one from South Carolina, and a few from Georgia. *Carex godfreyi* is moderately frequent only in Florida.

The geographic range of *C. godfreyi* only partially overlaps the collective range of the other members of the *C. grisea* complex, *C. godfreyi* occurring farther south. In fact, only *C. godfreyi* and *C. corrugata* are sympatric, from southeastern North Carolina to northern Florida. Though *C. godfreyi* and *C. corrugata* have been collected within a few kilometers of each other at a few localities (in Jones and New Hanover counties, North Carolina, and Gadsden and Leon counties, Florida), apparently they never have been encountered at the same site. Syntopy of *C. godfreyi* and *C. corrugata* is unlikely because of the preference of *C. godfreyi* for mucks and sandy loams and *C. corrugata* for clays.

I name this species for Dr. Robert K. Godfrey in recognition of his many botanical contributions and in gratitude for his assistance with my field work, especially for showing me the first plants I saw of this species. Through tireless collecting (including many of the specimens of *C. godfreyi*), training many students, and publishing numerous works on the vascular plants of the Southeast, Dr. Godfrey has exponentially increased our understanding of the flora of the region, particularly the area inhabited by *C. godfreyi*.

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EUPHORBIAE NOVO-GALICIANAE REVISAE

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More than 30 years ago I published an account (Brittonia 13: 167–187. 1961) of what I knew about the genus *Euphorbia*, at that time including *Chamaesyce*, from the part of western Mexico that is covered by the *Flora Novo-Galiciana*. Many new specimens have been collected since 1960, resulting in numerous range-extensions, and reports of species new to the area. The availability of more material for study, and recent revisionary papers by other authors, have made it possible – and necessary – to reconsider the taxonomy of some species-groups, and to describe what appear to be several taxa new to science. Data on some individual species are presented below essentially in the form of treatments in the Flora, with concentration on the same area. A map of Nueva Galicia, and an index to localities, may be found in *Flora Novo-Galiciana*, volume 17, pp. 436–453. 1992. For the privilege of large loans of herbarium material I am indebted to the curators and staffs at F, GH, MICH, MO, TEX, and US. Special favors of loans and information about types and other specimens at BM, HAL, and L were kindly provided by Roy Vickery, F. R. Barrie, Klaus Werner, and J. F. Veldkamp. Michael J. Huft has been especially kind in providing suggestions, information, and specimens relevant to this study.

As a belated apology to Sereno Watson, it should be noted that at least two of the new names that I published in 1961 were superfluous. My outlook at that time was even more provincial than it is now, and I neglected to look carefully enough to the north and east beyond the boundaries of Nueva Galicia, in order to match what I took to be novelties. In 1886 Watson (Proc. Amer. Acad. 21: 455) published the name *Euphorbia lineata*, based on *Pringle 187*, GH!, from borders of warm springs near Chihuahua. The plant has since been renamed *Chamaesyce lineata* (S. Wats.) Millsp. (Field Mus. Publ. Bot. 2: 410. 1916). It transpires that the same species occurs at widely scattered localities, always in wet places, south along the mountains to Durango and to Jalisco, whence I described it in 1961 as *Euphorbia paludicola* (Brittonia 13: 184). In 1891 (Proc. Amer. Acad. 26: 146) Watson proposed another new species, *Euphorbia misella*, from the State of Mexico, based on *Pringle 3305*, GH! This inconspicuous little plant, moderately widespread but scattered across central Mexico, and still little known, I redescribed as *Euphorbia biuncialis* (Brittonia 13: 172. 1961).

A BIBLIOGRAPHICAL NOTE ON THE *TRICOCCAE* OF KLOTZSCH & GARCKE

Modern students of the Euphorbiaceae often have occasion to refer to a paper by Klotzsch & Garcke, which consists primarily of a synopsis of the modern tribe *Euphorbieae*, or in a broad sense the genera *Chamaesyce*, *Euphorbia*, and *Pedilanthus*. Its importance today depends on the fact that the authors studied the

entire group. They recognized 18 genera of which they described 12 as new. They proposed almost exactly 100 new species and created several hundred additional new names and new combinations at the specific level. Several of their generic proposals have been accepted by subsequent authors. The newly proposed species, all or nearly all based on specimens in the Berlin Herbarium, are from all parts of the world, a majority of them from tropical America. At least 10 from Mexico are based on the collections of Carl Ehrenberg, a few on those of Schiede and Aschenborn.

An abridged version of the work was published in the report of the meeting of the Berlin Academy of Sciences of March 10, 1859, with the title, "Hr. Klotzsch las über Linné's natürliche Pflanzenklasse *Tricoccae* des Berliner Herbarium's im Allgemeinen und die natürliche Ordnung *Euphorbiaceae* insbesondere." (Monatsberichte Königl. Preuss. Akad. Wiss. Berlin 1859: 236–254. 1859 ["1860"]). Though the title-page of the volume bears the date 1860, the contribution by Klotzsch was noted as having been received in *Flora* for 7 Sep 1859.

In this preliminary version the author (Johann Friedrich Klotzsch) notes that he has undertaken the revision of the *Euphorbieae* in collaboration (*Gemeinschaft*) with his friend and colleague Herr Dr. [Christian August Friedrich] Garcke. All the new names published in this paper and in the later, more complete version, are attributed to "Kl. et Gke." and in later publications are properly attributed to both authors. The recent *Index Nominum Genericorum* cites them with nomenclatural pedanticism as "Klotzsch et Garcke in Klotzsch," and Oudejans (1990) as "Klotzsch & Garcke ex [J.] F. Klotzsch," though it may be argued that in a collaborative project the "in [or ex] Klotzsch" is unnecessary. The first half of the paper is devoted to a historical summary and to general taxonomic considerations of the Euphorbiaceae and related families. The second half includes descriptions of the newly proposed genera (*Trichosterigma*, p. 248; *Eumecanthus*, 248; *Tithymalopsis*, 249; *Dichrophyllum*, 249; *Leptopus*, 249; *Adenopetalum*, 250; *Medusea*, 251; *Arthrothamnus*, 251; *Sterigmanthe*, 252; *Euphorbiastrum*, 252; *Hexadenia*, 253; *Diadenaria*, 254) with summary comments on their geographical ranges and the number and names of the included species. One new species, *Euphorbiastrum hoffmannianum*, is proposed with a combined generico-specific description. In some genera, e.g., *Arthrothamnus*, *Eumecanthus*, *Medusea*, *Pedilanthus, Poinsettia*, some new combinations are validated by brief citations of the basionyms, but in most genera, as in *Adenopetalum*, the authors merely state, "Hierher gehören," followed by a list of binomials under *Euphorbia*, and a list of the names, without formal combinations or descriptions, of proposed new species of *Adenopetalum*. Many new combinations that were not in fact made at this time, but in 1860, are listed by Oudejans (1990) as if validly published in this 1859 article in the Monatsbericht. Stafleu & Cowan (Tax. Lit. ed. 2. 2: 571. 1979) cite two uncolored plates by C. F. Schmidt, *pl. 1–2*, accompanying the text of this 1859 paper. A reprint from the 1859 paper exists in the Stanford University collection of Adolf Engler's reprints, now at the California Academy of Sciences. It was reprinted on thick paper with the original pagination, pages 236–254, without change except for the deletion of the page-number on page 236, the deletion of the introductory material at the top of the same page, and the addition of a new title-page (recto, verso blank). Plates 1 and 2, by Schmidt, the only numbered plates in the volume of the *Monatsberichte* for 1859, accompanied a more ambitious paper by Klotzsch, on Aristolochiaceae, pp. 571–626, in the same volume, and were correctly so reported by Stafleu & Cowan. Evidently the citation of the same plates with the paper on *Tricoccae* was a gratuitous addition.

The more complete version of the *Tricoccae*, with descriptions of newly proposed species, and full documentation for all new names and new combinations, was published the next year with the same title, beginning "Linné's natürliche Pflanzenklasse *Tricoccae*" (Abhandl. Königl. Akad. Wiss. Berlin 1859 [Phys. Abhandl.]: 1–108. 1860). The *Physikalische Abhandlungen* do not constitute a separate series, but are included in the general volume along with the mathematical and philological/historical contributions, each of the three with its own pagination. The *Tricoccae* was again reprinted as a separate, apparently without any modifications except for the preparation of a new title-page (recto and verso) and changes in the first page that do not affect the text. Stafleu & Cowan (loc. cit.) mention the reprint and again cite "*pl. 1–2* (uncol. liths. by Franz Wagner)." In the copy of this volume of the *Abhandlungen* in the University of North Carolina library I find no mention of any such illustrations. My copy of the reprint lacks the plates. Ms. Bernadette Callery, Research Librarian at the New York Botanical Garden, kindly reports that neither of two copies of the reprint in that library includes the plates. In a copy at the Missouri Botanical Garden, however, which was sent to George Engelmann by A. Braun, as mentioned by Stafleu & Cowan, there are two such plates done by Franz Wagner. The Curator of Botanical Literature at the Garden, Ms. Linda L. Oestry, very helpfully informs me that the plates appear to have been tipped in, after some cropping, when the volume was bound. The plates are quite irrelevant to the text, representing two African species described by Klotzsch in Peters' *Reise nach Mossambique*, vol. 6, *Botanik*, in 1861, viz. *Cephalocroton mollis* (Peters, p. 99, *pl. 17*), and *Calyptrospatha pubiflora* (p. 97, *pl. 18*). Both species are euphorbiaceous, but not members of groups treated in detail in the *Tricoccae*. It may be surmised that the plates were bound in inadvertently, having been included by Braun with the reprint sent to Engelmann, or sent separately to Engelmann soon afterward.

For nomenclatural purposes the shorter article in the *Monatsbericht* has priority over the fuller account in the *Abhandlungen*. This affects the new generic names published by Klotzsch & Garcke, and the few new combinations under *Poinsettia* and other genera, but relatively few other names. Most of the new names proposed by these authors date from some unspecified time in 1860. I have no information as to the exact date, nor as to whether the reprint was distributed before or after the text of the volume itself. It would be useful to know the earliest date at which either one was published, in view of possible nomenclatural conflicts with Boissier's *Centuria Euphorbiarum*, also published in 1860, perhaps in April. In this paper Boissier mentioned (without any documentation) several Klotzsch & Garcke names that did not appear in their 1859 paper, which suggests that either specimens with annotations by Klotzsch & Garcke, or the text of their 1860 work, must have been available to Boissier before April 1860. In Boissier's account of *Euphorbia* published two years later (in DC. Prodr. 15, part 2, 1862), he cited the Klotzsch & Garcke names, this time with the addition of the page-numbers from the 1860 publication.

CHAMAESYCE AND *EUPHORBIA*

Whatever the disposition of smaller natural groups within the heterogeneous assemblage that is *Euphorbia*, its very size and heterogeneity have made it unwieldy. Webster (1967), in a superb and objective review of generic limits in this and other groups of Euphorbiaceae, said, "The tremendous diversity in habit,

leaf morphology, chromosome number, and pollen configuration might at first appear to favor the dissolution of *Euphorbia* into a number of smaller genera. However, a review of the taxonomic history of the Euphorbieae is sufficient to indicate that the problem does not have an obvious solution... If the various microgenera of Euphorbieae cannot be easily distinguished, there seems little reason to adopt them simply because they represent evolutionary units; it is quite as easy to discuss the evolution of these taxa if they are referred to as infrageneric components of *Euphorbia*." Webster then concluded (pp. 397–398) that much further study of the basic cytological and morphological data will be needed before the taxonomic impasse can be resolved. His solution, *pro tem.*, was to accept a compromise view on generic limits, a "disposition... frankly one of expediency and... not [claiming] either logical or phylogenetic justification." The compromise was ["diffidently"] to accept *Chamaesyce* as a distinct genus and relegate all other segregate taxa, including *Poinsettia*, to subgeneric status within *Euphorbia*. "*Chamaesyce* happens to be a large and doubtless natural group of several hundred species which is rather easily definable. It seems more convenient, in practice, to recognize *Chamaesyce* as an independent genus than to retain it within *Euphorbia*."

Marshall C. Johnston (1975, pp. 137–138), in a spirited rebuttal of Webster's view, argued that in spite of the fact that *Chamaesyce* is rather easily definable, it is still a weak genus and there is no compelling evidence to justify its removal from its traditional place in *Euphorbia*. He went on to say that although some taxonomists will probably continue to recognize *Chamaesyce* at the generic level, "inasmuch as most lay and professional botanists still use an inclusive concept of *Euphorbia*, the recognition of *Chamaesyce* as a genus is a latent if not actual impediment to communication, and is therefore inadvisable. The use of a broad concept of *Euphorbia* reaffirms an appreciation of the often benign role of inertia in scientific communication."

Though for the *Flora Novo-Galiciana* I personally would prefer to maintain *Euphorbia* in the inclusive sense, and I fully agree with Johnston that the dismemberment of such a large traditional group may be for a time a troublesome impediment to communication, reason tells me that if I follow my own recommendations for segregation of genera, as set forth previously (Wrightia 1: 15–17. 1945), I have to accept the alternative classification: 1) *Chamaesyce* has some marked morphological distinctions, in the abortive stem-axis and sympodial branching, and in the always opposite and usually inaequilateral stipulate leaves with their unusual chlorenchyma-sheathed veins. In Mexico a very few species (to be retained in *Euphorbia*) seem to cross the line between the two taxa, but it may be that further study will resolve the difficulty. As Webster noted, "the difficulty in writing an unequivocal generic diagnosis of *Chamaesyce* is real, but not greater in actuality than for many other euphorbiaceous genera." 2) *Chamaesyce* is not an unfamiliar name; it has been accepted by various authors at different times, and most of the combinations at the specific level, at least for species in Nueva Galicia, are already available. 3) Homogeneity. *Chamaesyce* is a large and natural group of some 250 species. 4) *Chamaesyce* is not merely an element of a local flora, but is worldwide, though a majority of the species (at least three-fourths) are American. In the *Flora Novo-Galiciana*, dealing as it does with an area in which at least two-fifths of the approximately 75 species of *Euphorbia*, *sens. lat.*, belong to *Chamaesyce*, the separation between the two genera should be a convenience to users of the Flora, and perhaps will lead eventually to a better under-

standing of both taxa. *Chamaesyce* once accepted, the following new combinations are necessary, and the following newly discovered taxa are placed on record:

Chamaesyce apatzingana (McVaugh) McVaugh, comb. nov. *Euphorbia apatzingana* McVaugh, Brittonia 13: 182. 1961.

Chamaesyce feddemae (McVaugh) McVaugh, comb. nov. *Euphorbia feddemae* McVaugh, Brittonia 13: 183. 1961.

Chamaesyce grammata McVaugh, sp. nov., ut videtur annua, prostrata, ramis petiolisque supra pubescentibus, subtus glabris; folia glabra (pilis paucis basalibus exceptis), ut videtur subcoriacea, opaca, laminis plerumque oblongo-ellipticis ubique uniformibus 5–9 mm longis, apice subserrulatis, basi inaequilateralibus; partes floriferae distales ramorum elongatae rectae, primo aspectu simplices, sed cyathiis in fasciculis compositis axillaribus quoque nodo orientibus; involucrum (glandulis exclusis) ca 0.5 mm longum; involucri glandulae 4, terminales, manifeste stipitatae, rotundatae, diametro 0.15–0.3 mm, appendicibus angustissimis; flores ♂ ca 5; styli 0.5–0.7 mm longi, bifidi; gynophorum crassum, vix quam involucrum longius; capsula 1.2–1.3 mm diametro, trilobata, pilis brevibus corrugatis dense vestita, loborum pilis in cristis tribus longitudinalibus aggregatis; columella ca 1 mm longa; semina ovoideo-quadrangularia, 0.8–0.9 mm longa, subroseo-brunneola, angulis acutis, superficiebus lateralibus transverse profundeque 4 (–5)-sulcatis.

Known only from the type-collection, taken in a region of low hills sparsely wooded with *Cordia*, *Amphipterygium*, *Cercidium*, and *Caesalpinia platyloba*, elev. ca 275 m, in a pasture ca "1 mi" west of San Juan de los Plátanos, between San Juan and Santa Ana Amatlán, Mpio. Apatzingán, Michoacán, with flower and mature fruit 17 Sep 1958 (*McVaugh 17960*, MICH, the holotype).

Prostrate herb, annual or of indefinite duration, with few branches 5–10 (–18) cm long spreading from a vertical taproot; branches forking or unilaterally branched near base, with internodes there often 1 (–2) cm long, the distal portions of the branches all straight and very floriferous, with few–15 or more rather crowded floriferous nodes on a seemingly unbranched axis, the distal internodes 2–5 mm long; stems compressed, thin-edged at least distally, the upper side convex and crisp-pubescent, the lower side flat or nearly so, glabrous except for a sparse fringe of marginal hairs; stipules distinct, subulate, reddish, those on the upper side very narrow (like setae), hispidulous, 0.4–0.6 mm long, usually (at least at the upper nodes) with the base of an abortive peduncle between them; lower stipules only sparingly hispidulous, well separated and often divergent, ca 1 mm long and up to 0.5 mm wide at base; petioles ca 1 mm long, puberulent or pilose on the upper side; blades glabrous except for a few long hairs at base, apparently subcoriaceous, thick with thicker pale margins, opaque, the venation usually not discernible in dried specimens; blades nearly uniform in size throughout (or those at the distal nodes slightly smaller), oblong-elliptic or slightly wider at base or apex, 5–9 mm long, 1.5–3 (–4) mm wide, mostly about twice as long as wide, the apex blunt and weakly to obscurely serrulate, the base moderately to strongly inaequilateral, obtuse to truncate or hemicordate; cyathia very crowded at fertile nodes in compound axillary clusters up to half as long as the leaves, the clusters sessile but sometimes dispersed along an axis up to ca 1 cm long with 5–8 internodes 0.5–1 mm long and reduced green bracts; cyathia 1–6 in an individual cluster; peduncles ca 0.5–1 mm long; involucres pilose distally, ca 0.5 mm long exclusive of the

glands; lobes erect, triangular, about as long as the glands; glands 4, erect, manifestly slender-stalked, terminal, standing 0.3 mm high including the stalk, nearly round, red, cupped, 0.15–0.3 mm across, the appendage usually a narrow abaxial rim up to ca 0.1 mm wide, below the gland; ♂ flowers ca 5; styles 0.5–0.7 mm long, bifid about one-third their length; gynophore scarcely longer than the involucre, ca 0.75 mm long, disproportionately thick (ca 0.25 mm), pilose distally, usually strongly recurved about at the margin of the involucre; capsule subglobose, shallowly and roundly 3-lobed, 1.2–1.3 mm in diameter, densely vestite with short white upstanding crumpled multicellular hairs, the hairs on the lobes in contrasting longitudinal bands, those in the intervals shorter and less densely crowded; columella ca 1 mm long; seeds pinkish brown, ovoid-quadrangular with prominent angles, truncate at base, acute at apex, 0.8–0.9 mm long, the faces 0.4–0.5 mm wide; all faces with ca 4 (–5) deep transverse sulci narrowed at bottom to a line, the intervening ridges rounded, extending to small protuberances at the four angles.

The specimens of this species were originally identified as belonging to *Euphorbia* (*Chamaesyce*) *thymifolia*, which they superficially resemble because of the prostrate stems and the small leaves. In that species, however, at least in our area, the proximal pair of appendages to the glands are commonly somewhat enlarged, wider than the gland is long, and sometimes prolonged distally 0.4–0.7 mm beyond the gland. More fundamental differences are in the seeds, in the gynophore, and in the vestiture of the ovary and capsule. In *C. thymifolia* the seeds are marked by shallow and often irregular transverse concavities separated by subacute ridges, the gynophore is so short that the capsule is never fully exserted from the involucre, and the capsule is thinly and evenly covered with straight or crisped hairs that do not obscure the surface.

Chamaesyce linguiformis (McVaugh) McVaugh, comb. nov. *Euphorbia linguiformis* McVaugh, Brittonia 13: 184. *figs. 16–18.* 1961. Type, Michoacán, Apatzingán, *Hinton 12014*, MICH, holotype and isotype; US, isotype.

This species is unique among the Mexican species of *Chamaesyce* known to me, in having the involucral glands oriented radially instead of transversely (tangentially). [The same orientation of the glands is reported in one rare species of the deserts of southern California and Arizona, *C. platysperma* (S. Wats.) Shinners, but in that species the seeds are strongly flattened and the glands are exappendiculate]. The relatively large cyathia of *C. linguiformis*, the elongate appendages, the large triangular-ovoid almost isodiametric but nearly unlobed capsule with truncate base, and the large quadrangular unornamented seeds also provide a distinctive combination of characters. I have seen nothing that precisely matches Hinton's original specimens of *Chamaesyce* (*Euphorbia*) *linguiformis*, which constitute the var. **linguiformis**. Though those were complete in the sense that all parts of the plant were present and could be described, they were brittle and broken and not easy to study.

Originally I failed to notice the unusual orientation of the involucral glands, though they are clearly shown in the illustration in the protologue (Brittonia 13: 175. *fig. 16.* 1961). Thirty years later, when I came across specimens with radial orientation of the glands, it seemed at first that these represented an undescribed species from the lowlands of Michoacán. Later, when I compared the description of this plant with a complete new description of *C. linguiformis* based on re-examination of the type-material, I could find no single character in which they differed

significantly except that the leaf-blades in *C. linguiformis* are always entire as far as can be determined, and those of the newly collected material are serrulate. Subjectively, Hinton's specimens do not look as if they were conspecific with the others, but that is a matter of taxonomic prejudice, not of fact. The two taxa share a unique combination of so many features that the new material is here presented as representing a variety of *C. linguiformis*, and is treated in full to allow adequate comparison with var. **linguiformis**:

Chamaesyce linguiformis var. **actinadenia** McVaugh, var. nov., herba perennis, prostrata, omnino glabra, stipulis conspicuis plus minusve coalitis 1–1.5 mm longis, foliis brevipetiolatis, laminis oblongo-ovatis vel oblongo-ellipticis 5–6 (–10) mm longis serrulatis, cyathiis in axillis vel furcis distalibus solitariis longe pedunculatis 1.5–2 mm longis, glandulis 4 radiatim elongatis, appendicibus linguiformibus; pedunculi 5–12 mm longi; involucri lobi rotundati, ca 0.5 mm longi, intus pilosi; glandulae terminales patelliformes, rotundatae vel latiores quam longiores, diametro 0.4–0.6 mm; appendices sub glandula ad angulum ca 90° patentes, niveae vel roseolae, 0.8–1.5 mm longae, 0.5–0.8 mm latae; flores ♂ ca 35–40; styli ca 1 mm longi, crassi, longitudinis dimidio bifidi, ramis capitatis; gynophorum 4–5.5 mm longum; capsula late ovoideo-triangularis, ca 3–3.5 mm longa lataque, basi truncata; columella 2.4–2.7 mm longa; semina 2–2.2 mm longa, grisea vel brunneola, oblongo-quadrangularia, laevia, basi truncata, superficiebus abaxialibus convexis 1–1.2 mm latis, adaxialibus subplanis 0.7 mm latis; a var. *linguiformi* foliis serrulatis differt.

Bare sandy Pacific beaches (the type collection) or "open grazed desert scrub," sea-level to 200 m as far as known, collected in early anthesis in July and with mature fruit in August.

Mich., Mpio. Aquila, "Playa Cocula about 44 miles SE of the Colima-Michoacán boundary on Route 200" (*R. L. Wilbur 36640*, MICH, the holotype); Mpio. Arteaga, valley of the Río Balsas, highway 37, "3.2 mi" S of La Vinata, "0.2 mi" S of Las Cañas (*W. W. Thomas 2935*, MICH). Otherwise unknown.

Perennial, glabrous and apparently glaucous, from a woody cylindrical root 15 cm long and 4–6 mm thick, the many slender prostrate branching stems 20–30 cm long from a crown bearing persistent stem-bases of a previous season; stems ca 0.5–1 mm thick near base, the internodes throughout the plant 10–40 mm long; leaves opposite; stipules united at least at base into a whitish triangular scale 1–1.5 mm long, with long-fringed tip and margins; petioles ca 0.5–1.5 mm long; blades oblong-ovate to oblong-elliptic, mostly 5–6 mm long and 2.5–4 mm wide, rounded abruptly to the petiole at base (at least in the larger leaves manifestly inaequilateral), rounded at apex, usually with a reddish streak near base adaxially on the midline, minutely (sometimes obscurely) serrulate on the distal half of the blade and sometimes nearly to the base especially on the longer side; cyathia solitary and long-pedunculate in the distal axils and forks, the peduncles 5–12 mm long, ca 0.25 mm thick; involucres funnelform or campanulate, usually acute at base, 1.5–2 mm long excluding the glands; lobes roundish, pale, ca 0.5 mm long and wide, with a few narrow teeth at apex, and hairy on the inner surface; glands 4, saucer-shaped, terminal and standing at approximately a right-angle to the long axis of the involucre, round or commonly elliptic, then with the longer axis radially oriented, the longer axis (width) 0.5–0.6 mm, the shorter axis (length) ca 0.4–0.5 mm; appendages linguiform, showy, white or pinkish, rounded at apex, entire, spreading widely from beneath the abaxial side of the gland, often curved upward

near the tips, 0.8–1.5 mm long, 0.5–0.8 mm wide; ♂ flowers ca 35–40; styles ca 1 mm long, stout, bifid about half their length, the branches capitate; ovary ovoid, subtruncate at base; gynophore 4–5.5 mm long, usually strongly recurved; capsule broadly ovoid-triangular, only obscurely 3-lobed, truncate at base, ca 3–3.5 mm long and wide; columella 2.4–2.7 mm long; seeds 2–2.2 mm long, smooth (without ornamentation), oblong-quadrangular, dull gray to brownish gray, truncate at base, obliquely obtuse at apex, keeled abaxially, the abaxial side more prominent and the faces convex, ca 1–1.2 mm wide; adaxial faces nearly flat, ca 0.7 mm wide with a strong median line between them.

The paratype specimen cited above consists of vegetatively vigorous young plants at an early stage of flowering, with most cyathia not yet fully developed, the appendages 1 mm long or less, but the glands showing clearly the radial orientation. The leaf-blades are somewhat larger than those of the type, up to 9–10 mm long and 5–6 mm wide, on petioles up to 2 mm long.

THE CASE OF *EUPHORBIA* (*CHAMAESYCE*) *DIOECA*

Kunth (in H. B. K. 2 [quarto]: 53. 1817) proposed the name *Euphorbia dioeca* for a specimen collected by Humboldt & Bonpland in Venezuela, "juxta Cura, alt. 226 hex. (Valles de Aragua)." He assumed the plant was dioecious, having found nothing but staminate flowers, and said of the specimen "Planta in statu vivo denuo examinanda," perhaps thinking that if living plants could be examined, the matter of the unisexual cyathia ("flowers" as he called them) could be investigated further. His description made it clear that the plant was a small prostrate pubescent species of *Chamaesyce* with two of the four glandular appendages larger than the others. Naturally enough he did not mention the seeds.

Since 1817 the name has been mentioned by various authors, mostly incidentally, usually with the spelling of the epithet changed to *dioica* (though there is considerable precedent for the other spelling, e.g., in the Class Dioecia of Linnaeus, and Kunth's spelling seems to have been intentional, as in his description he used the words *floribus dioecis*). Klotzsch & Garcke (1860, p. 31) made the combination *Anisophyllum dioicum*, stating at the same time that *Euphorbia multiflora*, no. 9291 of the Willdenow herbarium, was the same species. Boissier (in DC. Prodr. 15, part 2: 49. 1862) took up the name *Euphorbia adenoptera* Bertoloni, published in 1843, for an assemblage that included most of the American members of a complex of species having the glandular appendages in unequal pairs, as in *E. dioeca*. He implied that he had seen the original material of *E. dioeca*, as he wrote among his citations, "Venezuela (Humb. Bonpl.!), and he included the name *E. dioeca* ("*dioica*") in the synonymy of *E. adenoptera*. Presumably he discarded *dioeca*, the older epithet, because, as he wrote, "Nomen specificum Humboldtianum omnino improprium, involucrum enim omnia a me observata hermaphrodita." Boissier described the seed as "transverse et parallele 5–7-sulcato," but unhappily that description applies equally well to several members of the complex that have since been been segregated.

C. F. Millspaugh (1914) was the first person to provide a convenient means of separation of *Chamaesyce dioeca* ("*dioica*") (H. B. K.) Millsp., and four other species in our Flora, from *Euphorbia* (*Chamaesyce*) *adenoptera*, under which name Boissier (1862) had united them all. Millspaugh transferred all the species to the genus *Chamaesyce*. He distinguished individual species principally on the charac-

ters of the involucral appendages (whether present or absent, and if present whether glabrous or hairy), and the characters of the seeds; all the species have three- or four-angled seeds with more or less distinct transverse ridges and alternating hollows or furrows (sulci, in Millspaugh's terminology) on the lateral faces. The sulci in some species are said to be "open" (i.e., shallow concavities alternating with acute or narrow ridges), or "closed" (i.e., narrower than the alternating somewhat rounded ridges), or "closed to mere slits" (i.e., appearing as deeply sunken lines between broad rounded ridges). The extremes are easy to recognize but some intermediate states exist. Millspaugh found that of all the species *C. densiflora* was the easiest to recognize, having the glandular appendages hairy on the backs, and spreading hairs on the angles of the stem, these manifestly multicellular and usually with purplish crosswalls. The other species, namely *C. anceps*, *C. dioeca*, *C. inaequalis*, and *C. indivisa*, are not so easily separable.

According to Millspaugh's description, *Chamaesyce dioeca* is unique among these species in having long one-celled hairs on the stems and presumably on the leaves. He emphasized this point, but I have yet to find such hairs on any of his annotated specimens, or indeed on any other. His conclusion may well have been influenced by the fact that the hairs are perfectly colorless, not as in *C. densiflora* with dark walls between the cells, so the individual cells may be difficult to distinguish.

He described the seeds of *C. dioeca* as 0.6 mm long, with 4 closed transverse sulci of which the two basal ones are sometimes anastomosed, the surface of the seed-coat [microscopically] pitted, and the principal angles of the seed not tuberculate (as they are said to be in *C. indivisa*). I cannot say how he obtained this information about the seeds, as the holotype of *Euphorbia dioeca* was said to lack both fruit and pistillate flowers.

In support of his views, Millspaugh cited (1914) about 18 different gatherings representing *C. dioeca*, in addition to as many as two or three duplicates of the same collection, in different herbaria. I have studied seeds of 16 of the gatherings, including all those still at F and a few at MICH, finding to my surprise that two types of seeds are represented among them. All the specimens from Yucatán have seeds like the above (with deep pits and rounded intervening ridges), but only two others, one from the Pacific slope of Guatemala, the other from central Michoacán (*Gregg 812*). All the rest (10) of the collections cited by Millspaugh, from localities in Central America and both eastern and western mainland Mexico, have a different seed, easily recognized as such, in which the transverse ridges are acute and often reduced to a line (suggesting a fold in a sheet of paper), and alternate with shallow concavities round at the bottom. I have called these seeds rippled (or dimpled, when the concavities do not extend the width of the seed-face), in contrast to the seeds with deep pits narrowed at the bottom, and intervening rounded ridges.

This preliminary study led to a survey of the approximately 100 gatherings at F and at MICH, that have been filed under the name of *Euphorbia* (or *Chamaesyce*) *dioeca*, mostly because of their superficial similarity to one another. All plants are pubescent throughout, including the capsule and involucre, all were prostrate or nearly so, and all have glandular appendages in unequal pairs, glabrous or nearly so. It transpired that plants with the two types of seeds are neither randomly distributed nor are they sympatric.

The plant with deeply sulcate seeds, as noted above, is well known in the lowlands of Yucatán, but otherwise the relatively few Mexican and Central American collections all seem to be from inland localities at elevations of 500 m or more,

mostly 500–1800 m in Central America, 500–2300 in Mexico, where it is easily confused with *Chamaesyce indivisa* (e.g., *Gregg 812*, from Michoacán, cited by Millspaugh as *C. dioeca*). Until further study of South American material can be made, it seems best to keep the name *Chamaesyce dioeca* for this plant that fits Millspaugh's description, if the Mexican representatives of it can really be distinguished from *C. indivisa*. *Chamaesyce dioeca in* this sense is apparently unknown from Nueva Galicia.

The plant with "rippled" seeds has been much collected in lowlands on both coasts of Mexico, from Sinaloa and Veracruz southward, and abundantly throughout Central America at least as far south as Nicaragua. It seems to be absent from the Yucatán Peninsula. It is found on sea-beaches (where it is almost indistinguishable from *Chamaesyce thymifolia*), and commonly at elevations up to about 500–600 meters, rarely to 1000 or 1200 m. I have seen one collection from the interior of Chiapas, apparently from an elevation of about 2000 meters.

This plant is here tentatively referred to *Euphorbia anceps* Benth. (Bot. Voy. Sulph. 162. 1846; Nicaragua, Realejo, ?*Barclay*, K? or BM?, the type). I have not seen the type, and prefer not to make a formal nomenclatural transfer to *Chamaesyce* at this time, but contemporary Nicaraguan specimens referred to *E. anceps* appear to represent the same species. I cannot separate it satisfactorily from *C. dioeca* (*sensu* Millspaugh) except by the seeds. Millspaugh may not have been fully satisfied with his concept of *C. dioeca*, as he himself (p. 384) stated that "*dioica* is strongly mutational, hardly two specimens having been seen that exactly duplicate each other." Reports of *Chamaesyce dioica* from Sin., Nay., and Col., by Millspaugh, probably all refer to specimens of the present species, or perhaps to *C. thymifolia*. A thorough revision of these "vespertilloid" species is urgently needed.

NOVELTIES IN, AND COMMENTS ON, *EUPHORBIA, SENSU STRICTO*

Euphorbia caperata McVaugh, sp. nov. *Euphorbiae leucocephalae* Lotsy persimilis, sed involucris glandulisque majoribus; appendicibus suborbicularibus vel latissime ovatis ca 1.3–1.5 mm longis latisque, non anguste ovatis vel sublinearibus 1.5–2.5 mm longis et 0.5–1.1 (–1.5) mm latis; stylis paullo longioribus; ovario capsulaque crispe pilosis et confertim rugis tuberculisque carnosis parvisque obsitis (non laevibus glabrisque). Exempla in statu florendi non vidi. Fig. 1.

Forested hillsides near transition between oak-pine and tropical deciduous forest, with *Pseudosmodingium*, *Bursera*, *Lysiloma*, 1300 m in the drainage of the Río Tepalcatepec at the one known locality, with mature fruit 25 Oct.

Jal., Mpio. Tecalitlán, Mata de Bule, Sierra de Los Corales (*Feddema 2224*, MICH, the holotype and only known specimen).

Shrub ca 2 m high, the stem and petioles densely soft-pilose with grayish hairs up to ca 0.5 mm long; inflorescences and herbage similarly but less densely pilose; leaves and axillary branches whorled, 3–6-nate at major nodes of the branches, opposite in the inflorescences; petioles slender, flexuous, 2–4.5 cm long; blades elliptic, those of major leaves 6–8.5 cm long, 2–4 cm wide, obtuse or pointed, and very shortly emarginate at apex, acute or rounded at base, entire and somewhat revolute, dark green and thinly pilose adaxially, much paler (?glaucous) abaxially, densely pilose along the large veins and thinly so elsewhere; lateral veins ca 9–12 on each side; stipules glandiform, minute; cyathia in slender 1–2-forked or umbel-

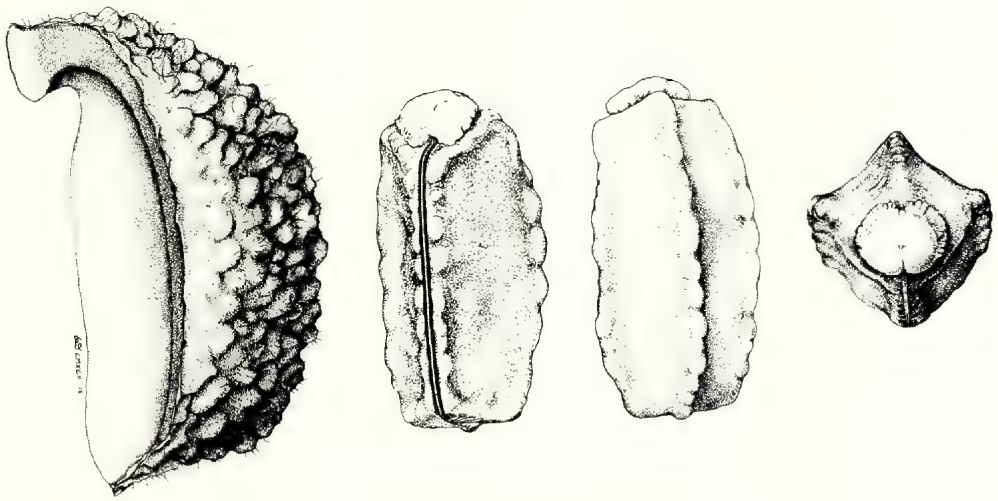

FIG. 1. *Euphorbia caperata* (from the holotype). Left-to-right, one-half of one carpel after dehiscence of the capsule, showing pilose and tuberculate outer surfaces, ×10; seed, ×10, adaxial view, abaxio-lateral view, and apical view.

liform cymes terminating the whorled axillary branches, these 10–25 cm long including the unbranched basal portion (5–) 9–13 cm long; bracts of the cymes narrowly elliptic, the larger blades 3–4 cm long, 1–1.5 cm wide, those of the ultimate branchlets 7–10 mm long, 3–4 mm wide, glabrous and sometimes red adaxially; specimens in flowering condition not seen; fruiting peduncles of cyathia 2–3 mm long, 1 mm thick; involucre (persisting and surrounding the gynophore) ca 1.5–1.7 mm long excluding the glands; lobes oblong or flabellate, 0.8–1 mm long, lacerate at apex; glands 5, transversely elliptic, 1–1.2 mm long, 0.6–0.8 mm wide (high), unequally concave at apex with the inner side shorter, erect, standing ca at right-angles to the appendage and seemingly arising from the inside of the appendage just above the base; appendages (presumably white) suborbicular to very broadly ovate, narrowed below the gland, rounded at apex, entire, reflexed in age, ca 1.3–1.5 mm long and wide; ♂ flowers numerous, apparently ca 25; styles glabrous, ca 1.2 mm long, stout, ca 0.2 mm thick, scarcely connate at base, thickened at the outcurved apex, bifid about half their length; gynophore 2.5–3 mm long, less than half its length exserted from the cyathium, 1 mm thick in fruit, erect; columella 4.5–5 mm long, often much dilated at apex; capsule subglobose, slightly 3-lobed, subtruncate at base, broadly rounded at apex, 6–6.5 mm high and wide, crisp-pilose, densely covered and roughened by small fleshy wrinkles and tubercles; seeds oblong, sometimes curved, gray with a dark adaxial line, acutely quadrangular, 3.7–4.3 mm long, the four sides equal or unequal in width, 1.5–1.8 mm wide; sides smooth, concave, the thickened angles smooth or commonly studded with up to 10 large pale tubercles; base truncate, the apex oblique, bearing a fleshy yellow peltate flattish caruncle 1–1.2 mm wide.

The type-collection has previously been identified with a Central American species, *Euphorbia leucocephala* Lotsy (Bot. Gaz. 20: 350. *pl. 24.* 1895, the four syntypes from Guatemala) to which it is very similar in most respects, and to which it is clearly closely related. A full and direct comparison of the two cannot easily be made, as flowering specimens of *E. caperata* are unknown, and I have been unable to locate fruiting specimens of *E. leucocephala.* In that species many

of the cyathia seem to produce staminate flowers only, as noted by Lotsy in the protologue. In examining 60 flowering specimens, I found pistillate flowers partially exserted from the involucre in 14 only, and in each instance only one or a few, sometimes on a specimen with hundreds of cyathia. Fortunately the involucres, glands, appendages, and styles are sufficiently well preserved in the existing specimens of *E. caperata* to permit some comparisons with a good series of specimens of *E. leucocephala*. The most striking difference is apparently that between the pistillate flowers and fruits of the two taxa. In *E. leucocephala* the ovary (and at least the immature fruit) are completely smooth and glabrous. Most flower-parts seem to be smaller in *E. leucocephala*; the styles in that species are slightly shorter (ca 0.8–0.9 mm long), the involucres only 1–1.25 mm long, the glands 0.5–0.8 (–1) mm long and 0.4–0.55 (–0.6) mm wide; the appendages vary from broadly ovate to nearly linear, from 1.5–2.8 mm long and 0.5–1.5 mm wide, thus from ca 1.8–3 (–4) times as long as wide. In the protologue of *E. leucocephala* it is stated the seeds lack a caruncle, but this is doubtful.

Originally *Euphorbia leucocephala* was based on four specimens, without any indication of type, all from Guatemala, viz. *Shannon 305* and *Heyde & Lux 3661, 3482,* and *6377*. Standley (Contr. U.S. Nat. Herb. 23: 603. 1923), presumably working under the American Code of Nomenclature, chose the first collection cited in the protologue as lectotype. He cited no collector, but stated that the "type" was from Cuilco, Shannon's locality; later (Fieldiana Bot. 24, part 6: 107. 1949) Standley & Steyermark designated *Shannon 305* as "type," i.e., lectotype. The specimen at US!, from John Donnell Smith's herbarium, is skimpy but readily identifiable.

Euphorbia creberrima McVaugh, sp. nov., a *E. furcillata* trichomatum minutissimorum creberrimorum indumento pallido, umbellis brevissimis 1–2 (–5) cm longis, radiis ca 5, 4–8 (–12) mm longis, involucri bracteis patentibus vel reflexis ovato-lanceolatis, antheris valde exsertis, pedicellis 0.8–1.4 mm longis, stylis longioribus (1.3–) 1.8–2 mm longis differt.

Grassy openings and along arroyos in dry oak-pine forest, 2200–2450 m in Nueva Galicia as far as known, in the northern part of the Santiago basin at the edge of the Central Plateau, found flowering (but mostly only ♂ flowers yet developed) in early November, fruiting in March.

S Dgo., n Jal. (Mpio. Mezquitic, 8–10 km SE of El Mortero, road to Monte Escobedo, Zac., near the Jal.-Zac. border, in shade of oaks, 2450 m, *Feddema 2452*, MICH, the holotype).

Dgo., Mpio. Mezquital, between El Durazno and Xoconostle, pine-oak forest (*M. González E. 1184*, TEX); Jal., Mpio. Mezquitic, 5 km E of Rancho El Mortero, forest of *Pinus lumholtzii* and *Quercus "macrophylla"* [i.e., *resinosa* ?], 2200 m (*Rzedowski 17695*). Rzedowski's collection and the type were taken from nearly the same locality; the Durango locality is about 100 km farther northwest. The species is otherwise unknown.

Described as a low shrub, the basal parts unknown, the inflorescences terminal on slender strongly ascending leafy branches 20–35 cm long, the branches woody, evidently arising as lateral offshoots from aborted stems of one or two previous years, the older leafless stems 2–3 mm thick with many old leaf-scars; herbage and branches very densely beset with innumerable and incredibly short erect pale trichomes, the longest of these on the twigs ca 0.2 mm long, those on the abaxial leaf-surfaces much shorter, and on the adaxial surfaces and the cyathia mostly reduced to mere papillae; cauline leaves very numerous for 10–20 cm

below the inflorescence (8–10 to each cm of stem, or on rapidly growing twigs only 2–3 to each cm), the older twigs naked with closely beset leaf-scars; blades spreading to markedly reflexed, narrowly lanceolate to elliptic or oblanceolate, 1.5–4 cm long, 3–6 mm wide, rather abruptly narrowed at base to a slender petiole ca 1 mm long, acute and mucronate at apex; inflorescences rather sharply differentiated at the tips of the leafy twigs, forming small corymbs 1–2 (–5) cm high and 1.5–4 cm wide, consisting of ca 5 rays in a small umbel subtended by an involucre of sessile, lance-ovate, spreading to reflexed bracts ca 12–25 mm long and 4 mm wide; rays 4–8 (–12) mm long, at apex 2 (–3)-forked, the cyathia ca (15–) 30–50 at the periphery of the corymb, on peduncles up to ca 1 mm long, the bracts at the forks broadly elliptic or obovate, acuminate, up to ca 8 mm long and 5 mm wide, the uppermost smaller; involucres about as in *Euphorbia furcillata* but mostly smaller, 1.3–2 mm long exclusive of the lobes and glands; glands 4, crescent-shaped, or scarcely curved and shaped like a flattened semicircle, 1.5–2.3 mm long, 0.7–0.8 mm wide (high), pointed at the ends but mostly not cornute, the distal margin entire or obscurely erose; ♂ flowers 20–30, at least the central ones much exserted (the tips of the androphores as much as 1.5–2 mm), the pedicels 1–1.4 mm long; styles (1.3–) 1.8–2 mm long, connate ca 0.7 mm at base, bifid about one-third their length, the tips subcapitate; ovary minutely papillose, the capsule essentially smooth; gynophore minutely papillose, 4–4.5 mm long, usually strongly recurved, the collar ca 1 mm wide; capsule broadly ovoid with 3 prominent rounded lobes, rounded and with depressions at both ends, wider than long, ca 3.5 mm long, 4–4.5 mm wide; columella 2.5–2.8 mm long, with 3 triangular acute projections at apex; seeds ovoid-oblong, 2.3–2.5 mm long, 1.5–1.7 mm in diameter, rounded at base, more or less terete with a well-marked adaxial line, obliquely angled at apex, with a flattish peltate caruncle 1–1.2 mm wide; surface smooth but mottled in a raised-reticulate pattern, dull brown with paler or whitish ridges.

In addition to the characteristic indument, this plant differs from most specimens of *Euphorbia furcillata* in the smaller corymbs that stand well above the leaves, in the longer styles and longer anther-pedicels. The relationship to *E. furcillata* is apparent in almost every feature. The latter is very variable in habit and in floral characters, and individual plants that exactly match *E. creberrima* in one character or another, except for the indument, are occasionally found.

Indument in this species, as described above (I hesitate to call it pubescence, because the individual trichomes in no way resemble ordinary hairs), is so dense as to give the herbage a grayish tinge, and so small that the individual trichomes (or papillae) can scarcely be discerned with a 10-power lens. Each epidermal cell is produced into an upright conical structure with large lumen and heavy lignified outer walls. Such structures are among those characterized by Metcalfe & Chalk (Anatomy of the Dicotyledons. ed. 2. 1: 152. fig. *10.13*, *e.* 1979) as intermediate between papillae and hairs[1].

These epidermal outgrowths in *E. creberrima* are almost incredibly like those of **Euphorbia ivanjohnstonii** M. C. Johnston (Wrightia 5: 129. 1975, the type from northwestern Coahuila, Sierra Santa Fe del Pino, *M. C. Johnston et al. 11237*, TEX!, the holotype). I have seen this collection, and the only other known collection, from the same mountain range (*I. M. Johnston & Muller 512*, TEX), through the kindness of Dr. Guy L. Nesom. Though this type of indument appears to be

[1] I am indebted to my colleague W. C. Dickison for demonstrating the internal anatomy of these epidermal outgrowths, and for calling the pertinent literature to my attention.

unique in this group of species, and indeed in Mexican Euphorbias in general, and perhaps indicates some distant relationships among the taxa that share it, there can hardly be any doubt that *E. ivanjohnstonii* and *E. creberrima* constitute different species. The former is apparently a shorter plant, subherbaceous except at base, with shorter, more nearly ovate and relatively much wider cauline leaves, the cyathia not confined to a distinct terminal corymb but in part lateral on short axillary shoots. The cyathia are similar in the two taxa, but in *E. ivanjohnstonii* the glands are less than half as large as those of *E. creberrima,* the ♂ pedicels are much shorter and (in the two known specimens) not long-exserted.

I have been influenced by the same feature, that is to say the presence of almost the identical indument in taxa that are well separated geographically, but not detected elsewhere in the variable *Euphorbia furcillata*, to treat *E. creberrima* as a distinct species coordinate with *E. ivanjohnstonii*, rather than as a variety of *E. furcillata.* Additional fieldwork in the range of *E. creberrima* might well provide new information about the species, its variability, and its relationships with *E. furcillata.*

Another species with indument nearly like that of *E. creberrima* and *E. ivanjohnstonii*, but a true shrub with large strongly cornute glands consisting chiefly of two divergent "horns" about 1 mm long, is **Euphorbia longicornuta** S. Wats. (Proc. Amer. Acad. 25: 161. 1890, the type from the summit of the Sierra de la Silla, near Monterrey, *Pringle 2545*).

Euphorbia graminea Jacq. Sel. Stirp. Amer. 151. 1763; Obs. Bot. 2: 5. *pl. 31.* 1767.

Various authors in floras of tropical America, where this species is widely distributed, have emphasized the extreme variability of what seemed to them to be a perplexing complex of weedy plants often described as perennials, much in need of taxonomic study. Ours seems to be a well-established native species, a common herbaceous plant in moist shady places, not especially weedy, annual or of short duration, mostly glabrous or at least not conspicuously hairy, not unreasonably variable, but showing in Nueva Galicia several identifiable facies. The complex would benefit from a thorough modern revision covering its whole geographical range. The following notes are based on study of a large series of specimens, including those identified as *Euphorbia graminea* at F, MICH, MO, TEX, and US.

It is quite clear that *Euphorbia graminea,* as that species is commonly understood by compilers of American floras, includes the type of *Euphorbia graminea* Jacq. The description in the protologue of that name (1763) is suggestive but provides no conclusive evidence of the identity of the plant that Jacquin had. Such evidence was supplied by Jacquin in 1767 (Obs. Bot. 2: 5. *pl. 31.*). There he referred to his earlier publication and added some comments [English version by R. McV.]:

"I called [this] *Euphorbia graminea* because it grows in meadows among grasses, which support [the] weak [stem]. The *icon* shows at natural size [*duntaxat*] a branch of the dichotomous plant. I added the corolla [i.e., the involucre], split open, unfolded and enlarged, the better to show the two glands and lobes, which is all it has."

The figure shows the upper part of a widely forking floriferous plant, with internodes about 15 cm long above the first fork, and the succeeding internodes about 6.5–8.5 cm long above the second forks, then loose terminal clusters of

cyathia with some exserted apparently immature fruits. The enlargement shows the inner side of the involucre, with two large rounded terminal appendages projecting well beyond the involucre (the glands proper not shown), and with conspicuous hairy lobes inside the glands. This agrees well with, and supplements, the original description (1763), in which the leaves were characterized as opposite, entire, lanceolate, acute, lustrous, one and one-half inches long, few, on petioles an inch long, and the plant itself as herbaceous, erect, weak, all green and dichotomous, slender, two to three feet high, with the *pedunculi communes* [that is to say, the long floriferous upper branches] terminal, dichotomous, erect, and slender. The fact that Jacquin mentioned and illustrated opposite leaves only, implies that he studied, and perhaps collected, no more than the tops of the tall plants growing among grasses, and failed to observe the presence of alternate leaves that may well have been concealed among thickly growing grasses, or may have already fallen from the plant.

Through the kindness of Dr. Roy Vickery and Dr. F. R. Barrie of the British Museum (Natural History) I have been able to examine a specimen at BM, from Jacquin's herbarium. No geographical origin is specified, but it may be the same specimen, from "Venezuela," that Boissier (1862, p. 54) reported as having been seen in Banks' herbarium (now at BM). The specimen now at BM could perfectly well have served as the model for the illustration published by Jacquin in 1767, consisting as it does of the upper part of a plant, twice forked, with long internodes and few-flowered cymes with small bracts. The cyathia are quite typical of *E. graminea* as commonly understood, with two prominent glandular appendages, and the small bracts are narrow and evidently were whitish when fresh.

Plants of the above description are known from many localities in northern Venezuela and Colombia, as far as known of annual duration, commonly with long forking upper branches and with two (as described by Jacquin) or four involucral glands. In some specimens the appendages are unusually large and rounded for the species, resembling those drawn by Jacquin. Similar plants are common throughout Central America and Mexico. I have no hesitation in including in the circumscription of var. *graminea*, as segregated below, all similar plants with either two or four glands.

In general I find few obvious correlations between the number of glands and any other feature, though in Nueva Galicia, as discussed below, it seems clear that the variation is not random. The number has been stated baldly by various authors, again following Boissier (1862), as 2–4. The number does indeed vary from 2 to 4 (even rarely from 1 to 5). Variation from 2 to 3, 2 to 4, or 3 to 4, may occur in the same plant. Observation suggests (though the truth should be ascertained through field studies) that well-developed cyathia that are terminal at major forkings of the branches, may be larger and with more glands than those that are more crowded near the tips of flowering branchlets. Examination of a large suite of specimens from Mexico, Central America, and northern South America, shows that plants with 4 glands outnumber those with 2 glands in many parts of the range, sometimes in a ratio of as much as 2–4:1. On the other hand, plants with 2 glands seem to predominate in parts of northern Colombia (the type-region) and Venezuela.

Growth-form is so much influenced by environment, and so dependent upon the age of the plant, that it is not in itself very useful in dealing with herbarium specimens. Plants growing among grasses and competing with them presumably tend to become more elongated and with fewer basal branches than open-grown

plants of sandbars and roadsides. Plants just coming into flower usually lack elongate branches. Although the var. *graminea* remains in this respect a loosely defined entity, a survey of the available specimens suggests that throughout the range the prevailing plant-habit is the one described by Jacquin, mostly an annual plant with long dichotomously branching upper branches and either 2 or 4 involucral glands.

Leaf-shape throughout the range of the inclusive *E. graminea* is highly variable. Various collectors in different parts of the range have noticed this, now taking linear-leaved and broad-leaved specimens from the same locality, sometimes without comment but evidently supposing them to represent the same species, then again assigning different collection-numbers to two extreme leaf forms. Although in some extreme forms the cauline leaves are all narrowly linear, and at the other extreme all broadly ovate to suborbicular, there is a recognizable sequence in most well-developed plants from broad or very broad leaves near the base of the stem to narrower or even linear leaves in the upper part, where the stem is repeatedly forked. This progression, and indeed even the presence of broader leaves on the lower part of the stem, may not be discernible in herbarium specimens, because collectors tend to take the upper parts of large bushy plants, at a time when flowering is well advanced, and the lower cauline leaves have fallen. In younger plants, on the contrary, all the leaves on a given specimen may be broad, whether or not the plant will eventually produce long upper branches bearing narrower leaves.

It is beyond the scope of this paper to undertake a revision of the species (or species-complex) much beyond the borders of Nueva Galicia. Several taxa closely similar to but perhaps actually conspecific with *Euphorbia graminea* have been proposed, as for example *E. montereyana* Millsp. (Bull. Torrey Bot. Club 16: 66. 1889, the type from the Sierra Madre near Monterrey, N. L., *Pringle 2069*, F!, the holotype). This is apparently a local entity of the sierras from Tamaulipas to Nuevo León, recognizable usually by the presence of four or five glands and relatively large white glandular appendages, but variable like the rest of the species in habit and leaf-form. In southeastern Mexico, and especially from Chiapas to Honduras and Nicaragua, there is an increasing prevalence of forms with conspicuous petaloid inflorescence-bracts and ternate leaves (sometimes difficult to distinguish from *E. ariensis* H. B. K., a plant primarily of south-central Mexico, or from *E. leucocephala* Lotsy, a primarily Central American species). I have characterized some of these in annotations as part of an unresolved "Central American complex" related to *E. graminea*. Many specimens in this geographical area are obviously from perennial plants, sometimes described by collectors as shrubs, with woody roots and with larger and heavier stems, often said to be 1–3 m high, than those of plants from central Mexico. Many specimens are densely pilose and often scabrellous. In the *Flora of Guatemala* (Fieldiana Bot. 24, part 6: 91–92, 102, 113. 1949) a "rough-hirtellous, pilosulous or glabrate" plant with pure white inflorescence-bracts was treated under the name of *Euphorbia scabrella* Boiss. (in DC. Prodr. 15, part 2: 55. 1862; Ic. Euph. 14. *pl. 32*. 1866, the five syntypes from Mexico and Central America), and *E. graminea* was treated as a distinct species, "usually more or less pilosulous with spreading or crisped hairs, often glabrate," with green inflorescence-bracts. In Nueva Galicia the heavy pubescence and the larger petaloid bracts do not appear to be correlated. Almost all our specimens, if not glabrous, are sparsely and softly pilosulous to some extent, and the bracts are usually white but often small and inconspicuous. As remarked above, the floral

bracts in Jacquin's specimen were certainly white, at most with a greenish midline, but definitely not green. The resolution of this problem, as remarked in the *Flora of Guatemala*, awaits a careful modern revision of the whole complex.

In Nueva Galicia the situation seems less confused, and there appear to be three principal variants that are treated below as two varieties and a form of *Euphorbia graminea*. The prevailing extreme, which I take to represent *Euphorbia graminea* in the sense of Jacquin, occurs in the Pacific lowlands, and is also well known at elevations up to 500–1200 (–1500) m above sea-level. This is the plant discussed just above under the name of var. *graminea*, in which the glands are four or here less often two in number, the leaves mostly ovate to narrowly oblong, the inflorescence divaricately forking with long internodes extending well above the larger leaves, the ovary and capsule glabrous, seldom papillose. Collectors rather seldom take the underground parts of plants, but about 20 specimens from our area have what appear to be annual taproots, with fleshy tuberiform or moniliform thickenings noted on at least six of these.

In relatively humid montane forests, mostly between 1000 and 2200 m above sea-level, the prevailing population is what has been called *Euphorbia galiciana*, here considered to represent a variety of *E. graminea*. The glands are commonly 4, at least the major leaves linear or nearly so, the inflorescence more or less strongly suffused with purple-red, and with long and strongly ascending forking branches, the ovary and capsule glabrous. Plants often flower the first year from a small taproot, but 8 out of 13 specimens include what appear to be persistent stem-bases from a previous year.

Finally, in the Pacific lowlands and found sparingly at inland localities up to an elevation of 1900 m, is a plant in which the glands are usually two in number, the leaves relatively broad (even the upper ones often ovate to rotund), the inflorescence often leafy without conspicuously elongate branches, and the ovary and capsule often minutely glistening-papillose. On the basis of the available specimens (20 in number) that include basal parts, the plants seem to be strictly annual. This is treated here as a form rather than a variety, because although in Nueva Galicia the distinctive habit seems to persist even in old fruiting plants, in other parts of the range of the species plants of similar appearance can usually be identified as immature individuals of var. *graminea.*

Intermediates between the above taxa are not rare. The extremes are here given the status of a form and two varieties, in order that they may be identifiable by means of the types, but final resolution of the complex, and better definition of the infraspecific taxa, must depend upon research in the future.

The distribution of the inclusive *Euphorbia graminea*, as mentioned in literature and as ascertained from material in herbaria, is summarized below and the following general description is intended to apply to the species as a whole, as represented in our area:

Son., s w Chih., Sin., Dgo., Nay., Gto., Jal., Col., Mich., Gro., Méx., Qro., Mor., D.F., Oax., Pue., Ver., Hgo., Tamps., N.L., Coah., Yuc., Chis.; Centr. Amer.; ?W. Ind.; n S. Amer. ([Colombia, Cartagena], *Jacquin*, BM!, the lectotype here designated, corresponding well with the illustration in Jacq. Obs. Bot. 2: *pl. 31.* 1767).

Annual or of indefinite duration, up to 1.1 m high, usually 50 cm or less, freely branched, the branchlets nearly glabrous or somewhat pilose to densely pilose (especially on the basal parts of the plant) with pale tapering flaccid hairs up to 1 mm long; leaves petiolate, moderately pilose or strigose with similar hairs, scabrid on the margins, alternate except for 1–3 pairs at the base of the stem and

those subtending forking branches of the inflorescence; blades entire, the principal ones (subtending alternate branches near mid-stem) usually largest, the lower ones commonly shorter and wider and often more obtuse at apex, the upper ones commonly narrower; stipules glandlike, up to 0.5 mm long, commonly very soon deciduous; stems and branches mostly 2–4-forked in about the distal one-third or only near the tips, the internodes sometimes much elongate and the cyathia in small and seemingly pedunculate terminal clusters subtended by very small petiolate obovate or spatulate to lanceolate or linear bracts, these white or pale green or white with a green midline, or tinged with pink or purplish red, 3–7 mm long and 1–2 (–3) mm wide; peduncles up to ca 15 mm long, the lateral ones, or all of them, usually much shorter; involucres campanulate or funnelform, (1–) 1.5–1.8 mm long excluding the appendages and lobes, sometimes strigose distally on the outer surface; lobes white, relatively conspicuous (sometimes as long as the appendages), oblong or quadrate, or rounded at apex, ca 0.7–0.8 mm long and wide, fimbriate at apex; glands transversely elliptic or rotund, 0.25–0.4 mm long, 0.1–0.25 mm wide (high), the bases of the appendages closely surrounding and enveloping them; appendages mostly thick and relatively stiff, internally sulcate and conforming to the shape of the gland, thus convex externally at base, green at base and sometimes along the midline, or all green, laterally and distally white or purplish (sometimes all purplish), commonly ovate or deltoid-ovate as seen from without, (0.3–) 1 (–1.6, or rarely –1.8) mm long, (0.4–) 0.6–0.9 mm wide; ♂ flowers ca 40 (–?50); styles 0.7–1 mm long, bifid two-thirds their length or nearly to the base; gynophore 2.8–4.5 mm long, straight or strongly recurved; capsule strongly 3-lobed, 2.5–3 mm long and 3–3.5 mm wide; columella 1.6–1.9 mm long, broadly winged; seed (1.3–) 1.5–1.7 mm long, 1.3–1.5 mm in diameter, gray or brownish rust-color to almost black, with 3–4 shallow angular pits in each of 6–8 (–10) longitudinal rows, the surface usually beset with many small brownish tubercles and the angles between the pits usually coarsely tuberculate.

1. Glands of the involucre usually 2 (seldom 3 or 4); ovary and capsule commonly very densely and minutely glistening-papillose; petioles of major leaves mostly 15–30 (–60) mm long, the blades ovate or elliptic to suborbicular, 2–5 cm wide, ca twice as long as wide, or up to as wide as long; inflorescence branches commonly forked near the tips only, the distal internodes 3–5 cm long or less, and the cyathia not much surpassing the foliage; from near sea-level to ca 1900 m. forma *foliosa*.
1. Glands of the involucre usually 4 (less often 3 or 2, rarely 1 or 5); ovary and capsule commonly smooth and glabrous, sometimes minutely scurfy; petioles of major leaves various; blades various; stems repeatedly forked throughout the upper one-third or one-half of the plant, the internodes above the forks elongated (up to 5–10 cm long or more), and the cyathia supported well above the foliage.
   2. Inflorescence (floral bracts, cyathium and appendages, gynophore and sometimes ovary, and anthers) more or less strongly suffused with purple-red; distal branches of the upper forks strongly ascending; petioles of major leaves 4–10 mm long; blades prevailingly linear to narrowly elliptic or oblong, those of major leaves at and below the lowest forks (2–) 3–6 (–10) cm long, (1–) 2–5 (–7) mm wide, (7–) 10–15 (–30) times as long as wide; leaves at the lowermost nodes of the stem if present small, elliptic to suborbicular, (0.3–) 0.8–2.2 (–3.5) cm long, 0.3–0.9 (–1.5) cm wide, mostly 1.2–2.5 (–4) times as long as wide; plants 20–50 cm tall, in humid montane forests, 1000–2200 m. var. *novogaliciana*.
   2. Inflorescence usually without purple-red coloration; floral bracts white or usually greenish abaxially or along the midline; appendages green at base and commonly along the midline, usually white distally and laterally; distal branches of the upper forks divaricate to ascending; petioles of major leaves (5–) 10–20 (–45) mm long; blades except sometimes those subtending the upper forks of the stem not linear, those of the major leaves

lanceolate or the lower ones ovate, 3–7.5 cm long, (1.5–) 2–3 cm wide, 1.6–3 (–5) times as long as wide; leaves at the lowermost nodes, if rarely present at flowering time, smaller than but not conspicuously different in shape from the other cauline leaves; plants often coarse, sometimes flowering when 20–50 cm tall, but often 80–110 cm tall; near sea-level to ca 1500 m, commonly in deciduous forest. var. *graminea*.

Euphorbia graminea forma **foliosa** McVaugh, f. nov., foliosa, foliorum laminis ovatis, ellipticis suborbicularibusve, 2–5 cm latis, duplo longioribus quam latioribus; foliorum majorum petioli 1.5–3 (–6) cm longi; inflorescentiae rami prope apices plerumque furcati, internodiis distalibus 3–5 cm longis vel brevioribus, cyathiis folia non multo excedentibus; involucri glandulae plerumque 2, raro 3 vel 4; ovaria capsulaeque plerumque densissime et minutissime puberulo-papillosae.

Ravines, moist or rocky slopes, stream valleys, sometimes in disturbed habitats, in tropical deciduous or subdeciduous forest, or barranca-forest with *Carpinus*, *Magnolia*, and *Quercus*, sea-level to 1900 m, most common at lower elevations on the Pacific slope, and inland to the high valleys of the Santiago basin, flowering Aug–Nov. Known chiefly from Nueva Galicia.

Sin., s Zac., Nay. (mountains "9.5 mi" W of Tepic, [road to Jalcocotán], *McVaugh 18943*, MICH, the holotype), Jal., ?Mich., ?Gro.

Zac., pastured hills "5 mi" SW of Jalpa (*McVaugh 18499*); Nay., mountains "10 mi" SE of Ahuacatlán, road to Barranca del Oro (*McVaugh & Koelz 805*); oak woods on volcanic rock, road to Compostela, 25 km S of Tepic (*Webster & Breckon 15678*, MICH, MO); 1 km N of El Cuatante, ca 40 km (airline) N of Puerto Vallarta, Jal. (*Feddema 2649*); in oak zone, 200 m, 11 km on road to Compostela, E of Las Varas (*Dieterle 3968*); Jal., Tequila (*Pringle 5443*, glands 4!); ca 3 km SE of Puerto Vallarta, canyon of Río Cuale (*Feddema 2524*); above La Cuesta, road to Talpa de Allende, below the pass, 800–1400 m (*McVaugh 20260, 21167*); west branch of Río de Talpa, "11–12 mi" S of Talpa (*McVaugh 20410*); Mpio. La Huerta, camino a Nacastillo, ca 9 km E of Juan Gil (*Lott 2662*); 16 km E of Ameca (*Lott 1285*, F); 3 km NE of Cd. Guzmán (*Cutler 4098*, F); mountains N of Lake Chapala, 1500–1900 m, between Jocotepec and San Juan Cozalá (*McVaugh & Koelz 345*, glands 4!); barranca of Río Verde, between Tepatitlán and Yahualica (*McVaugh 17364*); "2 mi" SW of San Juan de los Lagos, in a ravine (*McVaugh 17631*). All specimens at MICH except as noted.

Small flowering specimens that perhaps belong here are: Nay., Mpio. San Blas, ca "3 mi" E of Jalcocotán (*Norris & Taranto 14987*, glands 4); Jal., Mpio. La Huerta, Pueblo Careyes, ca 7 km SE of the Estación Biológica Chamela (*Lott 2685*, glands 5!).

Plants of this form are usually recognizable at sight by the broad leaves that extend nearly or quite to the top of the plant, without marked distinction in shape between cauline and bracteal leaves, and by the position of the cyathia, these little or not at all surpassing the upper leaves. Correlated with these features, but not entirely consistently, are the presence of two glands in the involucre and the presence of minute papillae that cover the ovary and persist to some extent on the capsule. The plants as far as known (15 specimens with basal parts) are always annual from a small taproot; there are no known reports of perennial roots, nor of tuberous thickenings in the roots.

The taxonomic standing of this entity is not clear. Young plants of *Euphorbia graminea* often begin to flower at a time when most of the original broader cauline leaves are present, and before any considerable elongation of the distal branches. Especially if the glands of the involucre are two in number, dried specimens of such plants exactly simulate f. *foliosa*. It is impossible to determine whether or not the branches would have elongated, with the production of narrower upper

leaves, if the plant had been allowed to continue its growth. Fully mature specimens of f. *foliosa*, however (e.g., *McVaugh & Koelz 805*), though the upper bracteal leaves are narrow, lack the conspicuously long internodes of var. *graminea*. It seems that the form has some reality as an entity at least in our area. Similar plants with mostly broad leaves, either with two or with four glands, and relatively little elongation of the flowering branches, occur sporadically throughout the range of the species. Field-study to determine the status of the form, in Nueva Galicia and elsewhere, would be desirable.

Euphorbia graminea var. **graminea**. *Euphorbia graminea* Jacq., as to type. *Euphorbia colimae* Rose, Contr. U.S. Nat. Herb. 1: 356. 1895. *Euphorbia graminea* var. *lancifolia* Millsp. Field Mus. Publ. Bot. 1: 372. 1898. *Euphorbia graminea* var. *virgata* Millsp. Field Mus. Publ. Bot. 1: 372. 1898. *Euphorbia longepetiolata* M. E. Jones, Extr. from Contr. West. Bot. 18: 55. 1933.

In Nueva Galicia in moist or moderately dry places, forest openings, rocky bluffs, deep ravines, sometimes on limestone, sometimes in disturbed habitats, tropical subdeciduous forest with *Orbignya*, *Hura*, and *Brosimum*, deciduous forest with *Cordia*, *Bursera*, and arborescent *Ipomoea*, sometimes in oak or pine forest, sea-level to 1200 (–1500) m, chiefly on the Pacific slope, flowering (Aug–) Oct–Dec.

Nay., Jal. (La Barranca, Guadalajara, *M. E. Jones 27514*, POM*!, holotype of *E. longepetiolata*; F*!, GH!, isotypes), Col. (Colima, *Palmer 1170* in 1891, US, holotype of *E. colimae*; F!, GH!, isotypes), Mich.; outside Nueva Galicia occupies essentially the range of the species: Yuc., Izamal (*Gaumer 969**, F!, holotype of var. *lancifolia*; US!, isotype); Tekax (*Gaumer 1128**, F!, holotype of var. *virgata*; US!, isotype).

Representative specimens from Nueva Galicia: Nay., steep mountainsides on the descent "19 mi" NW of Tepic, road to Mazatlán, Sin. (*McVaugh & Koelz 721**); Xalisco ("Jalisco") (*Ferris 5902*, US*); Jal., Mpio. Cabo Corrientes, 8.3 km from El Tuito, road to Ixtlahuahuey (*Ayala 352**); Mpio. La Huerta, near Estación de Biología Chamela (*Lott 1424*, MO*); hills between Bahía de Navidad and Bahía de Tenacatita, road to La Manzanilla (*McVaugh 21021*, ovary puberulo-papillose); coastal plain "4 mi" N of Bahía de Navidad, road to Autlán (*McVaugh 20816*); seaward-facing slopes "13 mi" SW of Autlán, "4 mi" below the highway pass, (*McVaugh 19894*); many other collectors; *Webster & Breckon 16060*, ovary puberulo-papillose); road to Mina de San Francisco, N of Autlán, disturbed hillsides (*Lott 2735*, ovary papillose); Puente Barranquitos, 700 m, 17 km E of Jal-Nay border (*Burch 5387*, MO*); 23 km NW of Magdalena (*Burch 5345*, MO); Mpio. Tlaquepaque, Barranca de Colimilla (*Díaz Luna 2614**); above Ahuacapán, ca "10 mi" SE of Autlán, road to Corralitos (*McVaugh 19550*); Sierra de Manantlán, E of [Rancho] Manantlán, ca "5400 ft" (*Wilbur 2055*); with *Curatella* and *Byrsonima*, 2 km N of Pihuamo (*McVaugh & Koelz 1385*); Mpio. Tecalitlán, Mata de Bule, near Los Corales (*Rzedowski 17491*); between Sierra de los Corales and Tepalcatepec, Mich. (*Feddema 2239*); Col., Colima (*Palmer 107* in 1897); eroded limestone ridge at km 204, ca "10 mi" SE of Cd. Colima (*McVaugh & Koelz 1459*); Mich., rocky slopes S of Lake Chapala, km 543, ca "8 mi" NW of Sahuayo (*McVaugh 18177**); Aquila, woods by the beach (*Hinton 12625*); Distr. Apatzingán, Aguililla (*Hinton 15297*); Mpio. Arteaga, 9 km N of El Infiernillo (*Lott 2002*, F, MO). The asterisk (*) denotes specimens found to have 2 (–3) glands in the involucres examined; the remaining specimens were found to have 4 glands. In *Gaumer 969* the number of glands appears to vary from 2 to 4.

This variety is more generalized than the preceding and following taxa; for the most distinctive features see the key above. The cauline leaves are intermediate in shape between those of var. *novogaliciana* and those of f. *foliosa*. The long slender fertile branchlets, usually with bracts noticeably different from the cauline

leaves, commonly extend well beyond the foliage, as in var. *novogaliciana*, but the branchlets tend to fork at a wider angle than in that variety, and the cyathia and small bracts are almost invariably white or green, without purplish coloration. The involucral glands are commonly 4 in number, and the ovary and capsule are often (but by no means always) glabrous, not papillose. The roots are often clearly annual, but of plants with basal parts (17 from Nueva Galicia), tuberous or moniliform thickenings in the roots are present or have been noted by collectors in about one-third of the specimens.

It is sometimes difficult to assign a young plant with relatively narrow leaves to one variety or another. One such specimen, from Jalisco, Mpio. Tamazula, near Agua Hedionda, at 1900 m in pine-oak forest (*Rzedowski & McVaugh 1150*), consists of flowering plants 15–25 cm high, with narrow but not linear cauline leaves 2–3.5 cm long and 4–8 mm wide. The habitat, the size of the plants, and the type of branching suggests a form of var. *novogaliciana* with unusually broad leaves, but the branches are divaricate, the cyathia and small bracts are green and white, not at all purplish.

Euphorbia graminea var. **novogaliciana** McVaugh, var. nov. *Euphorbia galiciana* McVaugh, Brittonia 13: 173. *figs. 19–21.* 1961, as to type.

Known chiefly from Nueva Galicia. Representative specimens were cited in Brittonia 13: 174. 1961.

Plants are usually recognizable by their small stature (stems mostly 20–50 cm high), the linear or nearly linear leaves, the very narrowly ascending flowering branches overtopping the leaves, and the presence of a pink or purplish red color in various parts of the inflorescence. The bracts of the cymes are usually much reduced and scarcely foliaceous but petaloid and conspicuous, the ultimate ones oblanceolate, ca 4–5 mm long and 1 mm wide. Plants often flower the first year from a small taproot, but they appear to be of indefinite duration; it is not uncommon (seen in 8 of 13 specimens with basal parts) to see the bases of old stems subpersistent above a somewhat heavier and apparently older root.

The choice of a new and more appropriate epithet instead of the original *galiciana* is sanctioned by the International Code of Botanical Nomenclature, Art. 60, which states that in no case does a name have priority outside its own rank.

Euphorbia ocymoidea L. Sp. Pl. 453. 1753.

This is a slender annual, originally described from Campeche, Mexico, widely distributed in Mexico and Central America, and comprising several geographically segregated varieties. From the lowlands of Tamaulipas and San Luis Potosí, the central foothills of the Atlantic slope of Veracruz, and northeastern Guerrero, to Central America as far as Panama, most plants are readily identified by the profusion of slender gland-tipped hairs on the young branchlets, and by the presence of five (less often four) glands in the involucre, and a pubescent ovary and capsule. On the Pacific slope of Mexico, from Sonora south to Michoacán and México and east to the highlands of west-central Veracruz (Mpio. Jalacingo), the Valley of Mexico, and Morelos, the prevailing form is a plant with few or no glandular hairs, short branches and small leaves, pubescent ovary and capsule, and four glands in the involucre. Finally, in a relatively small area on the Pacific slope in Jalisco and Michoacán, is a third variety in which the herbage is nearly glabrous, the ovary and capsule glabrous, and the glands five in an involucre. The species is not well known through modern specimens from the Yucatán Peninsula, but all

known examples are glandular-pilose, so it was not a surprise to find that the original specimens from Campeche were that way also. Of the three varieties here recognized, one has gone unnoticed since its description in 1913 at the rank of species, whereas most Mexican and Central American specimens have been referred to *Euphorbia ocymoidea* (as the oldest name at species rank), to *E. astroites* (if glandular-pilose), or to *E. subreniformis* (if Mexican).

1. Ovary and capsule glabrous; gynophore 3–5 mm long, very slender to capillary; branchlets not glandular-pilose; glands of the involucre 5; cyathium, glands, and appendages not or rarely reddish; stems diffusely branched from the first, the strong lateral branches often as long as the central axis. var. *barnesii*.
1. Ovary and capsule strigose or pilose; gynophore commonly 1–2.5 (–4) mm long, not conspicuously slender.
   2. Young branches copiously pilose with slender gland-tipped hairs; glands of the involucre usually 5, sometimes 4 in addition to a smaller one, or seldom 4 only; branching variable, the plants often diffusely branched with strong lateral branches as long as the central axis. var. *ocymoidea*.
   2. Young branches not copiously glandular-pilose, from nearly glabrous to sparsely pilose, sometimes with very sparse gland-tipped hairs on the internodes, often with a very few extremely short clavate hairs near the nodes; glands of the involucre 4, commonly reddish, the cyathium and appendages almost always with some reddish coloration; stem (except when injured) and the few large primary branches usually maintaining a strong central axis with short lateral branches all about the same length. var. *subreniformis*.

Euphorbia ocymoidea var. **barnesii** (Millsp.) McVaugh, comb. nov. *Adenopetalum barnesii* Millsp. Field Mus. Publ. Bot. 2: 377. 1913. *Euphorbia barnesii* (Millsp.) Oudejans, Phytologia 67: 44. 1989.

Euphorbia ocymoidea var. **ocymoidea**. *Euphorbia ocymoidea* L., as to type. *Euphorbia astroites* Fisch. & Mey. Index Sem. Hort. Petrop. 10: 44. 1845. *Euphorbia astroites* var. *heterappendiculata* Millsp. Field Mus. Publ. Bot. 1: 28. 1895.

There appears to be no incontestable way to typify *Euphorbia ocymoidea*. It is possible, or even likely, that Linnaeus never saw a specimen. In 1753 he took the name and the specific character from his own Dissertation on *Euphorbia* (species no. 14, 1752). He gave in both places a reference to van Royen ("Roy. Lugdb. 199"), and stated "*Habitat in* Campechia. *Houst[oun].*" He included no further description, nor did he cite any manuscript from Houstoun, though such a manuscript had been mentioned by van Royen in his *Florae Leydensis Prodromus* of 1740, a work to which Linnaeus contributed.

No specimen of *E. ocymoidea* has been recorded from any Linnaean herbarium, as far as I am aware, and apparently none exists in van Royen's herbarium in Leiden, as Dr. J. F. Veldkamp kindly informs me. The only Houstoun specimen that I have been able to locate is one at the British Museum (BM), apparently the specimen cited by Boissier (in DC. Prodr. 15, part 2: 57. 1862) as "Houston in h. Banks!" It appears to have been taken from a plant cultivated by Philip Miller at the Chelsea Physick Garden. It bears a label in Houstoun's hand, "Tithymalus americanus, annuus erectus, ramosissimus, ocymi caryophyllati foliis. C Mss." and the further inscription "ex H[ort.?] Ch[elsea ?].: 1732." There is no evidence that Linnaeus ever saw the specimen. The herbage is copiously glandular, as in other specimens referred here to the var. *ocymoidea*, and the glandular appendages are cleft into narrow but not filiform divisions, as in many other specimens from Yucatán and elsewhere in eastern Mexico. Taxonomically I should refer it without question to the var. *ocymoidea* as differentiated in the key above.

If Linnaeus ever saw a specimen of *E. ocymoidea*, as explained below, it seems most likely that it was a duplicate of the one at BM, i.e., one presented to him by Miller, taken from a cultivated plant. In this case the specimen at BM is arguably an isotype and could be designated as lectotype. Whatever the case, there can be hardly any doubt that the Linnaean name derives directly from a plant of this particular gathering by Houstoun. In the absence of proof of the existence of a holotype, the specimen at BM is hereby designated as **neotype** of *Euphorbia ocymoidea* L.

Discussion: Philip Miller presented some of Houstoun's Central American and West Indian specimens, conceivably including a specimen of *Euphorbia ocymoidea*, to Linnaeus when the latter was in England in 1736 (Stearn, intr. to Ray Soc. ed. of Sp. Pl., 1957, p. 105). At the same time Miller gave to Linnaeus a series of Houstoun's unpublished notes (Stafleu & Cowan, Tax. Lit. ed. 2. 2: 343. 1979). Linnaeus then returned to Holland, where among other things he worked with Adriaan van Royen during the preparation of the latter's *Prodromus*. That either Linnaeus or van Royen ever saw a specimen of *E. ocymoidea* remains conjectural, but it seems clear that both saw a Houstoun manuscript, as one was cited in 1740, in van Royen's *Prodromus*, in a paragraph following the specific character, as follows: "Tithymalus americanus annuus erectus ramosissimus, ocymi caryophyllati folio. *Houst. mss.*" Presumably the words "ocymi caryophyllati folio" were Linnaeus's inspiration for the epithet *ocymoidea*, and it will be noted that the reference to "*Houst. mss.*" exactly repeats the words, with slight variations in spelling and punctuation, that appear in Houstoun's hand on the specimen at the British Museum. It is still not clear to me how Linnaeus hit upon Campeche as the source of Houstoun's material, for the locality was not cited by van Royen, nor does the word appear on the specimen at BM. For assistance in locating and assessing the significance of the Houstoun specimen, for information about the inscriptions thereon, and ultimately for the loan of the specimen, I am much indebted to Dr. F. R. Barrie and to Dr. Roy Vickery.

Euphorbia ocymoidea var. **subreniformis** (S. Wats.) McVaugh, comb. nov. *Euphorbia subreniformis* S. Wats. Proc. Amer. Acad. 21: 439. 1886.

Euphorbia oppositifolia McVaugh, sp. nov. sect. *Agalomatis*, perennis, erecta, ca 45 cm alta, omnino glabra; caulis foliosus, apicem versus 3–5-furcatus, ramis oppositis divaricatis; folia infra furcas omnia opposita, paribus ca 15, internodiis 0.7–3 cm longis; stipulae ut videtur in protuberationem planam coalitae, inter foliorum pares sistentes; petioli tenuissimi 5–8 mm longi; laminae anguste obovatae vel ellipticae, integrae, 3–4 cm longae (infimae minores), 1–1.4 cm latae, basi subattenuatae lateribus congruentibus, apice obtusae apiculatae; nervus medius subtus prominens subteres; lamina in paginis ambabus marginibusque minute papillosa, venis lateralibus debilibus obscuris; inflorescentia bracteata, bracteis foliosis viridibus, folia caulinia simulantibus sed minoribus 5–15 mm longis, plerumque ellipticis vel anguste ovatis; cyathia solitaria, in ramorum furcas distales terminalia breviter pedunculata; involucrum campanulatum 1–1.2 mm longum; lobi inconspicui, ca 0.3 mm longi, basi virides, apice albidi laciniati; glandulae 4 (–?3), conspicuae, planae, transverse elongatae, 0.3–0.5 mm longae, 0.2 mm latae; appendices virides, sub anthesi recurvatae, 0.4–0.7 mm latae, marginibus rotundatis integris, ultra glandulam ca 0.25 mm extensis; flores ♂ ut videtur 10–12; styli sub anthesi ca 0.5 mm longi, subcapitati, ad medium bifidi; gynophorum 1.5–2.5 mm longum,

FIG. 2. *Euphorbia oppositifolia* (from the holotype). Habit, ×0.5; terminal leafy node with pedunculate cyathium, ×15; involucre laid open, ×20; ovary and styles, ×20.

plerumque valde recurvatum; capsula submatura valde acuteque lobata, 1.9–2.2 mm longa, 3 mm lata; columella 1.3 mm longa; semina immatura ecarunculata, ovoidea, grosse foveata. Fig. 2.

Known only from the holotype, a somewhat less than satisfactory specimen: Jal., Mpio. Puerto Vallarta, entre El Arroyo Verde y El Nogal, en una cañada, 850 m, in flower and immature fruit 7 Nov 1971 (*R. González T. 590*, MICH).

Stem ca 45 cm tall, near base ca 1.5 mm thick, smooth, hard, arising from what appears to have been a multinodal horizontal rhizome ca 2 mm thick, with thin brownish bark splitting in irregular interconnected longitudinal fissures; leaves all opposite, ca 15 pairs, present at all but 3 of the lowermost cauline nodes; lower internodes 7–10 mm long, the upper 8 internodes 2–3 cm long; at each node, exactly between the bases of the petioles on opposite sides of the stem, are a pair of flattened hard triangular processes that I interpret as being stipular remains; petioles very slender, 5–8 mm long; blades entire, membranous, narrowly obovate or elliptic, all except the smaller lowest ones 3–4 cm long, 1–1.4 cm wide, subattenuate and bilaterally symmetrical at base, obtuse and apiculate at apex; midnerve prominent beneath, the lateral veins weak, obscure; blades minutely papillose at margins and on both surfaces; stem forking about 3–5 times in the apical 15 cm, the branches very slender, the cyathia few, terminal in the ultimate forks, on peduncles ca 1 mm long, subtended by broad green leafy bracts 5–10 (–15) mm long; involucre campanulate, 1–1.2 mm long; lobes inconspicuous, ca 0.3 mm long, green at base, whitish and laciniate at apex; glands 4 (?–3), conspicuous, transversely elongate, 0.3–0.5 mm long, 0.2 mm wide (high), somewhat flaring from the summit of the involucre, large in proportion to the appendages, flattened to the base of the appendage but raised platelike above the surface; appendages recurving from the involucre, a strong green when dry (sometimes darker than the leaves), apparently fleshy, roundish, entire, 0.4–0.7 mm wide, longer than the lobes of the involucre, but surpassing the gland proper by only ca 0.25 mm, little more than the width of the latter; ♂ flowers apparently 10–12; styles at anthesis ca 0.5 mm long, subcapitate, bifid ca one-half their length; gynophore 1.5–2.5 mm long, usually strongly recurved; capsule (somewhat immature) strongly and acutely lobed, 1.9–2.2 mm long, 3 mm wide; columella 1.3 mm long; seeds ecarunculate, when immature but nearly full size suggesting those of *Euphorbia graminea*, ovoid, with several longitudinal rows of shallow isodiametric depressions.

To base a description of a species on a single specimen without fully mature fruit or seeds is ordinarily to be avoided, and the description itself must be accepted as a provisional one. This is an extraordinary species, differing in a number of respects from any other Mexican or Central American species known to me. The combination of an erect, completely glabrous perennial with a hard and perhaps woody but still slender stem, numerous pairs of small opposite papillose bilaterally symmetrical leaves, green foliaceous floral bracts, four glands with short green appendages hardly twice as long as the width of the proportionately large glands, but still longer than the inconspicuous lobes of the involucre, and a small number of staminate flowers, appears to be unique. In habit the plant suggests some herbaceous species of *Phyllanthus*, under which name it was found in the herbarium.

Euphorbia schlechtendalii Boiss. Cent. Euph. 18. 1860; DC. Prodr. 15, part 2: 60. 1862. *Alectoroctonum ovatum* Schlecht. Linnaea 19: 252. 1846, not *Euphorbia ovata* E. Mey., 1843.

The name *Alectoroctonum* was proposed by Schlechtendal for a group of species now generally referred to *Euphorbia*, mostly woody plants with verticillate leaves and brittle nodes, widely distributed in Mexico and Central America. Standley (1923) admitted to the flora of Mexico about ten species of this complex, including *Euphorbia schlechtendalii*, which was distinguished from all the others (except for *E. peganoides*, which has linear leaves) in having the involucres glabrous and the appendages "nearly obsolete." Standley gave the range of *E. schlechtendalii* as "Tamaulipas to Sinaloa, Oaxaca and Yucatán," Guatemala, and Nicaragua;

that is to say, more or less throughout central and southern Mexico including Nueva Galicia.

It requires little more than a cursory survey to show that *E. schlechtendalii* is neither a homogeneous population, nor is it continuously distributed across Mexico from east to west. Like the other woody Mexican Euphorbias with verticillate leaves, it seems to find its best expression in the humid mountains facing the oceans both to the east and to the west. *Euphorbia schlechtendalii* itself seems to range almost continuously southeastward along the Pacific slope from Sinaloa to the Isthmus of Tehuantepec and beyond, and from the isthmus northward along the Atlantic slope to Tamaulipas. Within this range certain regional differences are manifest. Whether or not such regional variants are to be considered as mere curiosities, as named infra-specific taxa, or as distinct species, is almost always a subjective matter depending upon personal judgment. In this instance I believe it is reasonable to refer most of the individuals with glabrous involucres, throughout the range, to an inclusive *E. schlechtendalii*, with the possible exception of those constituting *Euphorbia macvaughii*, which was segregated in 1981.

In most specimens of what has been called *Euphorbia schlechtendalii* the branchlets, at first green, turn a rich reddish brown by the end of the growing season. Woody branchlets of one or more years of age, on drying, tend to shrink and become fluted, like some architectural columns, with longitudinal rounded grooves alternating with narrow acute ridges. The grooves tend to be irregular and anastomosing, but characteristic. The surfaces are not wrinkled between the ridges. At the nodes, and on older twigs, the surfaces often split or crack, with resultant loosening of a paper-thin red outer layer.

In some local variants, as in *E. macvaughii*, the older branches exfoliate in thin lustrous coppery-red papery layers, as in the genus *Bursera*, sect. *Bursera*.

The only major departure from the above, as far as noted, is in a population inhabiting the humid mountains of the Pacific slope, at elevations from about 1400 to 2600 meters. In this, apparently the most common representative of the species in Nueva Galicia, the woody twigs older than those of the current season remain terete in drying; the outer bark is gray to beige or pale reddish, not fluted but finely longitudinally wrinkled, usually not cracking longitudinally (as if stretched), and not exfoliating.

Among the specimens with dark red fluted twigs, I cannot always reliably distinguish those native to the Atlantic slope of Mexico (the type-region of *E. schlechtendalii*) from specimens with similar twigs from the Pacific slope at moderately low elevations (sea-level to 600 meters). Other features, however, tend to be concentrated in one region or the other, leading me to put forth the following scheme including *E. schlechtendalii* and its closest relatives:

1. Woody twigs (older than those of the current season) drying terete, the outer bark gray to beige or pale reddish, smooth or finely and sharply longitudinally wrinkled, usually not cracking longitudinally (as if stretched) nor exfoliating; leaves persistent more or less throughout the year, the inflorescences developing at the tips of branches when the leaves are full grown or nearly so; cyathia commonly numerous (up to 50 or more) in terminal umbelliform clusters; bracts subtending the cyathia scarious, subulate, deciduous from a prominent persistent base before the cyathia are fully developed; humid montane forests, 1400–2600 m. *E. schlechtendalii* var. *pacifica*.

1. Woody twigs in drying commonly fluted or angled, usually with strong acute ribs and broad concave furrows, dark reddish brown, the thin outer layers of bark (after the first year) often splitting longitudinally as if stretched, later often cracking and loosening near nodes,

in some populations readily exfoliating in thin coppery-red sheets; leaves persistent or deciduous, the plants often flowering when leafless; cyathia often fewer, sometimes numerous, the bracts quickly deciduous or persistent and leafy; plants of lower elevations, sea-level to 1200 (–1850) m.

2. Inflorescences developing on leafless branches, or with and slightly before the new leaves; bracts subtending the nodes of the cymes mostly caducous, or partly or wholly persistent and foliaceous; bark of the trunk and larger branches coppery red, conspicuously exfoliating; leaf-blades elliptic-ovate to obovate, broad at apex, often broadly cuneate at base, mostly 2–3 cm long and (0.9–) 1.2–1.8 times as long as wide.
   3. Flowering as the new leaves develop, or seldom on leafless branches; bracts subtending the nodes of the cymes often partly foliaceous and persistent, partly scarious, subulate, caducous; gynophore 1–1.5 mm long, the capsule never fully exserted from the cyathium; mostly inner valleys, sometimes on limestone, Jal., Col., 750–1850 m. *E. macvaughii* Carvajal & I. R. Lomelí.
   3. Flowering on leafless branches, rarely with developing leaves; bracts subtending the nodes of the cymes mostly scarious, subulate, caducous; gynophore 5–6 mm long, the capsule evidently exserted; valleys of the Pacific slope, 650–1500 m, Nay., Jal., Mich., Gro., Mor. *E. macvaughii* (var. ?).
2. Inflorescences developing on leafy branches after the leaves are fully grown, or shortly before that; bracts subtending the nodes of the cymes often all foliaceous (sometimes very small), and persistent; bark of the trunk and larger branches not conspicuously exfoliating as far as known; leaf-blades prevailingly ovate-triangular, widest at base, strongly narrowed to an acute (sometimes blunt) tip, 2–4.5 (–6.5) cm long, mostly 1.5–1.8 (–2.25) times as long as wide; capsule manifestly exserted.
   4. Cyathia mostly few–10, rarely to 30, in divaricately forking assemblages with a strong central peduncle, and most of the nodes leafy-bracted; moderately dry deciduous forests, sea-level to 600 m on the Pacific slope. *E. schlechtendalii* var. *websteri*.
   4. Cyathia in leafy-bracted cymes, or the branches elongating, more irregularly branched, only a few bracts leafy; 200–400 m as far as known, Atlantic slope, Tamaulipas to Veracruz. *E. schlechtendalii* var. *schlechtendalii*.

Euphorbia schlechtendalii var. **pacifica** McVaugh, var. nov., a var. *schlechtendalii* et a var. *websteri* differt: Ramulis in siccitate teretibus, viridi-griseis, pallide rubellis vel pallide brunneolis, nec angulatis nec striatis canaliculatisque fusco-rufis; cyathiis saepe numerosis, usque ad ca 50 in fasciculis terminalibus paniculiformibus vel umbelliformibus aggregatis; cymarum bracteis nec foliaceis nec persistentibus, sed earum apicibus scariosis subulatis mox deciduis; habitat in temperatis humidis Mexici occidentalis locis. A var. *websteri* foliis plerumque ellipticoovatis non triangulari-ovatis facile distinguitur. Fig. 3.

Mexico, common in western Jalisco (Sierra de Manantlán, along a stream, N slopes ca 24 km by road S of El Chante, near Rancho Manantlán, *McVaugh 23070*, MICH, the holotype) and western Michoacán, on mountainsides and in humid *barrancas* in pine or pine-fir forest or forest of mixed coniferous and deciduous trees, at elevations from 1400 to 2600 m, flowering November to March.

Specimens Examined (all at MICH except as noted): Jal., Mpio. San Sebastián [del Oeste] (*Mexia 1441*, US; Segundo Arroyo, *Mexia 1544*, GH, MICH, US); San Sebastián to Bufa de Mascota (*Nelson 4099*, GH, US); Mpio. Talpa de Allende (SW of Talpa, Sierra de Cuale SW of the peak called Piedra Rajada, *McVaugh 14365*; "10–12 mi" S of Talpa, above Los Sauces, headwaters of east branch of Río de Talpa, *McVaugh 21470*); near Santa Mónica, ca 20° N, 104° 30' W (*McVaugh 14055*); Mpio. Autlán, Sierra de Cacoma, 1500 m (*Limón & Puga 11712*, WIS); Mpio. Autlán, Sierra de Manantlán, Las Joyas (Vázquez *3810, 3894*, ZEA, reported by Vázquez *et al.* 1991, not seen); Sierra de Manantlán Occidental, La Calera (a ravine 9 km by air NNE of Casimiro Castillo) (*Iltis 31027*, MICH, WIS); SSE of Autlán, "4–10 mi" above Ahuacapán, road to Corralitos (*McVaugh & Koelz 940*); Sierra de Manantlán, seaward-facing slopes between Aserradero San Miguel Uno and

El Durazno, 2000 m (*McVaugh 13936*); Mpio. Tolimán, 3–4 km SSE of La Laguna, ca 39 km NW of Cd. Colima (*Cuevas & Nieves 2212*, WIS, ZEA); Mich., 15–16 km SE of Aserradero Dos Aguas, and nearly W of Aguililla, on limestone (*McVaugh 24738*).

This plant is common and conspicuous on the Sierra de Manantlán, as suggested by the numerous collections cited. As noted on the label of the holotype, it is probably the most common tree of the understory there, in barrancas and other humid areas. Two sterile specimens from arid regions near Apatzingán, Michoacán, *Leavenworth 1529*, *1544*, both F!, reported under the name of *Euphorbia schlechtendalii* in Amer. Midl. Nat. 36: 177. 1946, probably belong not here but with var. *websteri*.

Shrubby or arborescent, glabrous, sometimes with whiplike stems 1–4 m high and up to 1 cm in diameter, but often a copiously branched tree up to 10 m high and trunk-diameter of 12–15 cm, with verticillate leaves and branches, the leaves 3–6 (–8) in a whorl; woody twigs (older than those of the current season) remaining terete in drying, the outer bark gray to beige or pale reddish, finely and sharply longitudinally wrinkled, usually not cracking longitudinally (as if stretched), not exfoliating; petioles disproportionately slender, up to 0.5 mm thick, those of the principal leaves (1–) 3–5 cm long, often longer than the blades; blades entire, commonly elliptic-ovate, narrowed (usually from below the middle) to a broad obtuse and often slightly retuse tip, acute to broadly rounded at base, 2.5–3.5 (–7) cm long, 1.5–2.5 (–4) cm wide, 1.5–2.5 times as long as wide, the thickened margins often decurrent on the inner angles of the petiole or seldom forming a continuous line across it and the blade then subpeltate; principal lateral nerves ca 8 (–12) on each side; stipules glanduliform, broadly subulate, 0.2–0.6 mm long; plants flowering when in full leaf; inflorescence seeming to be of sessile axillary or terminal clusters, each cluster actually of several short-peduncled densely aggregated dichasial or irregularly branched naked cymes (the small subulate bracts soon deciduous above a conspicuous persistent base); peduncles 1.5–3.5 (–6) mm long; cyathia up to 5 in each cymelet, and up to ca 50 in a terminal cluster, short-campanulate, rounded at base, 1.9–2.6 mm long excluding the glands; lobes membranous, whitish, erect and relatively conspicuous, incurved in the young cyathium, 1.3–1.5 mm long and wide, quadrate or flabellate, fringed at apex; glands 5, green ("dull salmon-green"), transversely elliptic, cupped, 1.2–2 mm long, 0.5–1 mm wide (high); appendages fleshy, crowded and somewhat overlapping, radially spreading, yellow-green, cream-colored or "greenish cream," oriented and shaped like the glands but wider and longer, (1.3–) 2–2.5 mm wide, (0.3–) 0.7–1.5 mm long (high), entire or the margins sometimes sinuous or obscurely erose; ♂ flowers ca 20–35; styles ca 2 mm long, the basal column 0.6–0.8 mm long, the branches thick, ca 1.2–1.3 mm long, bifid one-half to two-thirds their length; gynophore (3–) 5–7 (–10) mm long, with prominent collar up to 1.5 mm wide; capsule (3.5–) 4.5–5 mm long, 5–6.5 mm wide, with 3 rounded lobes ca 3 mm in diameter; seed not seen mature, reported as 2.5 mm long (or as much as 3–3.5 mm), gray to dull brown, ovoid, truncate at base, 8–10-sided with 4–6 deeply concave pits on each face, the intervening ridges somewhat tuberculate and often paler.

Euphorbia schlechtendalii var. **schlechtendalii**. *Alectoroctonum ovatum* Schlecht., and *Euphorbia schlechtendalii*, as to type. Fig. 3.

Hillsides in moderately dry deciduous forest, often in calcareous or shaly soils, at low elevations on the Atlantic slope of Mexico and southward into Central America, flowering October to March. Reported from the states of Guerrero,

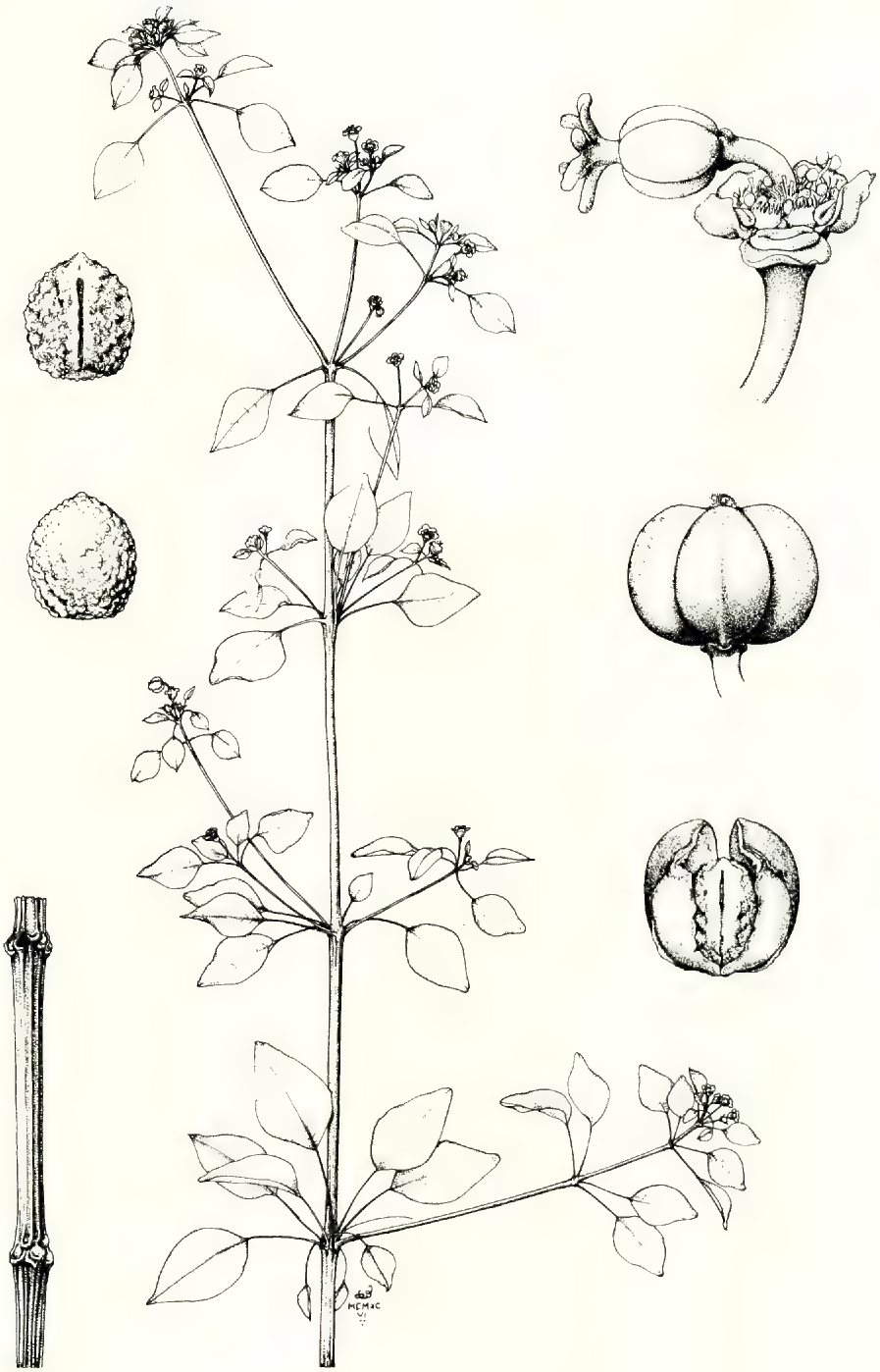

FIG. 3. *Euphorbia schlechtendalii.* Var. *websteri,* flowering branch, ×0.5 (from the holotype); seed, adaxial (upper) and abaxial views, and seed included in carpel after partial dehiscence, all ×5 (*Webster & Breckon 16067,* Colima). Var. *pacifica,* cyathium, lateral view, ×5, and capsule just before dehiscence, ×4 (both from the holotype). Var. *schlechtendalii,* portion of flowering branch, ×1, showing manner of shrinking upon drying (*M. C. Johnston 5235,* Tamaulipas).

México, Puebla, Veracruz (sylvis prope Actopan et sepibus Papantlae Mexici, *Schiede* in Jan and Mar 1829, the type; HAL!, the holotype), Hidalgo, Tamaulipas, and Yucatán and from Central America. What I take to represent the holotype, at HAL, which I have seen through the courtesy of the Curator, Klaus Werner, is mounted on two sheets. Sheet 71001, Bogen 1/2, bears a single copied label apparently partly in the hand of A. von Chamisso, and sheet 71001, Bogen 2/2, bears two original labels by Schiede, one for each locality. Each sheet includes several fragments both large and small, but as far as I can tell all the material on both sheets might have come from the same gathering.

Judging from the type-material, and from the limited amount of other material I have seen, the branchlets are indistinguishable from those of var. *websteri*; the leaf-blades tend to be rounded-ovate rather than triangular-ovate, mostly about 1.5–1.6 times as long as wide; the small bracts subtending the small cymes (that is, beyond the ultimate leafy cauline node from which the major cymes arise) are occasionally leafy and persistent, but never, as far as known to me, so consistently so as in var. *websteri*.

Euphorbia schlechtendalii var. **websteri** McVaugh, var. nov., frutex vel arbor glabra, var. *schlechtendalii* similis ramulis fusco-rufis, in siccitate angulatis vel striatis canaliculatisque, ramorum truncique cortice non desquamanti; sed foliorum laminis ovato-triangularibus vix elliptico-ovatis, apice plerumque acutis vel subacutis, inflorescentiae bracteis foliaceis, persistentibus differt; cyathiis paucis, fasciculo 5–15 (raro –30) aggregatis; glandium appendicibus plerumque integris, nonnunquam erosis; stylis subdistinctis vel in columna 0.2–0.6 mm longa coalitis; habitat in calidioribus Mexici occidentalis locis. Fig. 3.

Tropical deciduous forest with *Bursera*, *Acacia*, *Amphipterygium*, *Cordia*, *Senna*, sometimes with *Brosimum* or *Cephalocereus*, sometimes in transition from grassland to oak savannah, or on ocean bluffs, sometimes on limestone, from sea-level to 600 m in the Pacific lowlands and foothills of Mexico, flowering October to March.

Sinaloa, ?Nayarit, Jalisco (near Los Arcos, ca "2.5 mi" S of Río de Cuale in Puerto Vallarta, *Webster & Breckon 15785b*, MICH, the holotype; *15785a*, WIS, isotype), Colima.

Specimens Examined (all at MICH except as noted): Sin., Mpio. Elota, NW of Elota, ca 24° N (*Webster & Breckon 15650*); Jal., seashore 2 km S of Puerto Vallarta (*Rzedowski 17739*); Mpio. La Huerta, Rancho El Paraíso, Chamela, rocky point above the shore (*Lott 645*); Mpio. La Huerta, vicinity of the Estación de Biología, Chamela (*Lott 1592*, reported by Lott [1986] as *E. schlechtendalii*, not seen); Mpio. Cihuatlán, along the old (1951) road to Tequezquitlán, "15 road miles" N of Barra de Navidad (*McVaugh 18888*); "8 mi" SW of Pihuamo, on limestone, with *Brosimum* (*McVaugh & Koelz 1499*); Col., "14 mi" WNW of Santiago, road to Cihuatlán, Jal. (*McVaugh 20773*); near Manzanillo (*Lott 855*, *Webster & Breckon 16067*); Mpio. Colima, 5.5 km SW of Los Asmoles, Colima–Manzanillo highway (*Lott 353*); mountain summits ca 15–20 km SSW of Colima (*McVaugh & Koelz 1591*, *McVaugh 26199*).

Glabrous, mostly described as a shrub 0.5–2 (–3) m high, sometimes as scandent, or a "vinelike shrub 6 m long, 2 cm in diameter at base," often as treelike, or as a small slender tree 2–6 m high, 2–3 cm in diameter at base; resembling var. *pacifica* and often identified as such, but differing as follows: plants seemingly smaller on the average, more slender, and more sparingly branched; branchlets (after the first year) dark reddish brown, when dry fluted or angled, usually with

prominent acute ribs and round-bottomed furrows, the thin outer layers of bark often splitting longitudinally into interrupted or interlocking strips, later cracking and loosening near the nodes, but not reported as exfoliating from the large branches and trunk; petioles 1–2.5 (–4.5) cm long, commonly shorter than the blades; blades prevailingly ovate-triangular, broadest at base, acute at tip or sometimes (especially near the tips of the branchlets) ovate with broad obtuse tip, broadly rounded to obtusely angled at base, 2–4.5 (–6.5) cm long, 1.5–2.7 (–4) cm wide, mostly 1.5–2.25 times as long as wide; margins seldom decurrent at the base of the blade, sometimes meeting at the base on the adaxial surface; plants flowering when in full or nearly full leaf; cymes more leafy and with fewer cyathia than in var. *pacifica*, the number of cyathia in a cluster ca 5–15 (–30); bracts subtending the cyathia foliaceous but sometimes very small, shaped like the leaves or some of them elliptic, petiolate, persistent, the blades 1–5 mm wide; peduncles of the central cyathia of a dichasium up to 8 mm long; appendages 1.3–1.5 (–2.2) mm wide, 0.7–1 mm long (high), scarcely exceeding the glands or much larger, usually entire-margined, sometimes erose; styles essentially free to the base, or joined into a column 0.2–0.6 mm long, the branches ca 1–1.3 mm long, bifid two-thirds their length or a little less; gynophore 5–9 mm long; columella clavate, winged at apex, 2.6–3.3 mm long; seeds gray to nearly black, ovoid to subglobose, scarcely angled, truncate at base, 2.5–2.7 mm long, 2.5 mm in diameter, pitted on all surfaces, bearing adaxially a strong dark line.

What appears to be a variety or a close relative of *Euphorbia schlechtendalii* is **Euphorbia nelsonii** Millsp. (Bot. Gaz. 26: 268. *fig.* 1898, the type from María Madre Island, *Nelson 4284*, May 1897, US, the holotype, not seen). Other collections from María Madre and from Isla Isabel suggest that *E. nelsonii* may be a somewhat modified insular representative of the complex, resembling var. *websteri* with respect to the inflorescence but the leafy bracts fewer and less conspicuous, and the blades of the cauline leaves consistently orbicular-ovate or orbicular-obovate, 5–15 (–20, according to Millspaugh) mm long and 5–10 (–14.5) mm wide, on very slender (almost capillary) petioles usually longer than the blades (up to twice as long). The cyathia and the floral parts are generally smaller than in var. *websteri*; the columella is only about 2 mm long, and the seeds 1.8–2 mm long. The branchlets in drying become fluted, grayish red instead of dark red, and Mrs. Ferris noted that the "bark [is] gray, peeling off in thin strips as in fruit trees." A sample of the bark preserved with *Ferris 5609* indicates that the strips tend to peel off transversely, as in such fruit trees as peaches, cherries, and plums. I should refer the following to *E. nelsonii*:

Nay., Islas Tres Marías, María Madre (*Maltby 130*, *144*, May 1897, both US); María Madre (*Ferris 5609*, Oct 1925, US); Isla Isabel (*J. T. Howell 10532*, Jul 1932, US; *C. Davidson 2066*, Apr 1973, MICH).

Euphorbia tenuissima M. E. Jones, Extr. from Contr. West. Bot. 18: 55. 1933.

Marcus Jones (*loc. cit.*) proposed two new species of *Euphorbia*, *E. longepetiolata* with cited type *Jones 27514a*, and *E. tenuissima* with cited type *Jones 27514*, both from "La Barranca, Guadalajara." As noted by L. C. Wheeler (1945, p. 108) the published data do not agree with those on the specimens in Jones' herbarium at POM. The specimen that bears the name *longepetioliata* and is the plant so described by Jones [i.e., *E. graminea* var. *graminea* in the sense of this paper], is numbered 27514. The material that Jones described as *E. tenuissima* is mounted

with a label for No. 27538, a number that Jones cited under *longepetiolata*. There is no specimen bearing the number 27514a. Wheeler designated as "type," i.e., holotype, *Jones 27538*, POM. He stated that in his opinion the species was closest to *Euphorbia subcaerulea* Rob. & Greenm.

What Wheeler did not mention, and presumably did not notice, is that the material mounted on the type sheet includes adequate and entirely identifiable specimens of three quite different species. The description by Jones, in the protologue, emphasized especially the habit and small leaves of one species, the glandular appendages of a second, and the seeds of the third. The mounted specimens include 1) two plants of *Euphorbia delicatula* Boiss., a larger and a smaller flowering plant, both with roots; 2) one incomplete plant of *E. graminea* Jacq. var. *graminea*, with a root but with only a few flowering branches from midstem or below; and 3) a few detached leaves apparently belonging to *E. ocymoidea* L. The packet mounted on the sheet contains several fragments 2–5 cm long, with leaves and fertile cyathia, of *E. ocymoidea* var. *subreniformis*. It also contains numerous seeds of *E. delicatula* and of *E. ocymoidea*, and a few of *E. graminea*.

Jones' description precludes the choice of the *ocymoidea* element as lectotype, although he alludes to the resemblance between that species and his *E. tenuissima*, and called the plant a "weak and erect and almost capillary annual, easily mistaken for subreniformis." Unfortunately he described the "flowers" as "very small, with very short and whitish appendages entire and rounded." He apparently noticed the appendages of the *graminea* element, which fit that description admirably, but not those of *E. delicatula*, which are thin and purplish and hardly to be characterized as "very short." Of the seeds he first said, "oblong and rounded at both ends, and a little flattened, but rounded on the corners, and shallow-pitted in vertical lines, not angled." That is exactly the seed of *E. delicatula*, except that he failed to note the conspicuous caruncle, which has indeed fallen from most of the seeds in the packet. At the end of the description he added, as if as an afterthought, "Seeds pectinately warty and pitted," a characterization that loosely fits either *graminea* or *ocymoidea*, the seed of the former however much larger than the other.

If the name *Euphorbia tenuissima* is to be typified at all, it seems that it must be on the *graminea* element or the *delicatula* element, Jones having disqualified *subreniformis* by his description of the appendages, which in *E. ocymoidea* var. *subreniformis* are greenish and deeply dissected into narrow segments. He described the appendages of *graminea* adequately, and may be said to have added a short description of the seeds, although that description applies equally well to the seeds of *E. ocymoidea*. He described the seeds of *delicatula* separately, and that very well indeed.

Wheeler, even though he seems to have noticed only the one species on the type-sheet, effected a kind of informal lectotypification by his reference to *Euphorbia subcaerulea*, a name that in the *Flora Novo-Galiciana* (ined.) is treated as a synonym of *E. delicatula*. Since the largest part of the material on the type sheet of *E. tenuissima* consists of two well-preserved flowering plants of *E. delicatula*, and a large number of the very characteristic seeds (including caruncle) of that species, formal action seems in order, and the lectotype is hereby designated as POM 191023, plants marked A^1 and A^2. I am very grateful to the authorities at Rancho Santa Ana Botanic Garden for the loan of this and other specimens from POM.

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THE SPECIES OF GIANT SENECIO (COMPOSITAE) AND GIANT LOBELIA (LOBELIACEAE) IN EASTERN AFRICA

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INTRODUCTION

The giant senecios and giant lobelias from eastern Africa have been cited as examples of adaptive radiation (Mabberley 1973, 1976; Carlquist 1974; Nordenstam 1978; Stott 1981; Beck 1986). Members of each group occupy a range of montane habitats on each of the tall mountains in eastern Africa. The giant lobelias have a more extensive geographical and ecological range than the giant senecios. The lobelias are found at higher latitudes and lower altitudes, and relatives are found elsewhere in the tropics (Knox et al., in press). There has been extensive convergent evolution within each group, a situation which Mabberley (1973) described as a "mosaic of variation." There has also been extensive convergent evolution between the two groups, and with tropical alpine plants elsewhere (e.g., *Espeletia* in South America and *Argyroxiphium* in Hawaii), which provides compelling a priori evidence that the unusual features of these plants constitute adaptations to the peculiar climatic regime of "summer every day, winter every night" (Hedberg 1964).

My dissertation research has focused on the reconstruction of evolutionary history for the giant senecios and the giant lobelias. Each of these two case studies has been pursued using several lines of research including extensive fieldwork, phylogenetic analysis of morphology, restriction-site variation in chloroplast and nuclear DNA, chromosome counts, biogeographic analysis, and biochemical analysis of compounds in leaf tissue and secreted fluids. Monographic treatments for both of these groups are in preparation. In the interim, the need has arisen for revised taxonomies so that some facets of this project may be published with a consistent use of names prior to publication of the monographs. Presented below are brief discussions of the taxonomic history and problems within each group, along with a checklist of species and intraspecific taxa. Eleven species of giant senecio and twenty-one species of giant lobelia are recognized. Two new species and three newly recognized subspecies of *Lobelia* from Tanzania are described. Thirteen new combinations are proposed in *Dendrosenecio* and three new combinations in *Lobelia*.

THE GIANT SENECIOS

Hoffmann (1894) established *Senecio* section *Arborei* to accommodate the newly discovered *S. johnstonii* (Johnston 1886) along with woody species from Madagascar, Cameroon, Fernando Po, and St. Helena. Section *Arborei* was subsequently

purged of all but the East African species by Muschler (1909), independently emended by Humbert (1935), and renamed as subgenus *Dendrosenecio* by Hauman (1935). Hauman's description in French did not constitute valid publication after January 1 of that year, and so, Hedberg (1957) provided a Latin diagnosis to validate the name. Hauman distinguished subgenus *Dendrosenecio* primarily on life-form, and the inseparability of this group from the remainder of *Senecio* based on floral characteristics has been stated repeatedly (Cotton 1944; Hedberg 1957; Mabberley 1973, 1974a). Nordenstam (1977) revised the generic limits of *Senecio* and elevated *Dendrosenecio* to generic status (Nordenstam 1978), citing such features as "the pyramidal-paniculate synflorescence, the more or less biseriate involucre, and the continuous stigmatic surfaces of the disc styles." Jeffrey (1977) initially included the giant senecios in *Senecio*. He questioned Nordenstam's removal of the group (Jeffrey 1979), and classified the giant senecios as series *Arborei* in section *Crociseris* (Jeffrey 1986). In his most recent checklist, Jeffrey (1992) recognized the genus *Dendrosenecio* (Hauman ex Hedb.) B. Nord., and placed it in a primarily neotropical group of senecionoid genera in subtribe *Senecioninae*.

The segregation of *Dendrosenecio* is supported by evidence from DNA (Knox and Palmer, unpubl.) and biochemistry (Bohlmann & Knox, unpubl.) that demonstrates the lack of close relationship between the giant senecios and a narrowly delimited genus *Senecio*. The question concerning the origin of the giant senecios is currently unanswered, but the uniformly high chromosome number (n = 50) and the lack of meiotic irregularities (Knox & Kowal, in press) suggest that polyploidy in this group was not a recent event. Other segregate genera placed near *Dendrosenecio* (Jeffrey 1992) that include species with n = 50 may offer a starting point in the search for close relatives.

The taxonomic treatment of the giant senecios at the level of species and below is also complicated. The nature of colonial exploration in eastern Africa contributed to a proliferation of species descriptions such that most species were treated as narrow endemics. The size of the plants presented problems for collectors and resulted in many inadequate herbarium specimens (Hauman 1935; Hedberg 1957; Knox, in press). Adding to the confusion were erroneous descriptions of habit and habitat, and mixed collections such as those by J. W. Gregory from Mt. Kenya. E. G. Baker described Gregory's specimens as *Senecio keniensis* (Baker 1894a) and *Lobelia gregoriana* (Baker 1894b) with the leaves of the specimens switched (see Baker, 1894b, for an artist's reconstruction of one of these "species"). Fries and Fries (1922a, 1922b) rejected these names as nomina confusa, and from their own material renamed these species *S. brassica* and *L. keniensis*. As discussed by Thulin (1983a), the International Code of Botanical Nomenclature does not permit rejection of the original names, because satisfactory lectotypes can be selected from the original elements.

Hedberg (1957) discussed the taxonomic problems posed by the giant senecios, and reduced to synonymy several species based on minor vegetative differences or geographic separation. He also stressed the need for "comprehensive field studies by a botanist who has previously thoroughly mastered both the herbarium material available and the relevant literature." Mabberley (1973) addressed this problem as part of his dissertation and decided that the amount of differentiation was insufficient to maintain seventeen taxa of specific rank. His solution was to preserve the most distinctive species, *Senecio keniodendron*, to treat *S. brassiciformis* as a subspecies of *S. brassica*, and to submerge the remainder in a system of eight subspecies (and two varieties) in the highly polymorphic *S. johnstonii*.

Although Nordenstam (1978) disagreed with Mabberley's evolutionary interpretation based on Corner's (1949, 1954a, 1954b, 1964) Durian Theory, he considered Mabberley's taxonomic conclusions to be sound, and made no modification when he transferred the species to *Dendrosenecio*. However, Mabberley (1986) recognized earlier errors and reinstated *S. brassiciformis* at specific rank as *D. brassiciformis*, recognized *D. brassica* as a synonym of *D. keniensis*, and emended *D. johnstonii* subsp. *refractisquamatus* as *D. johnstonii* subsp. *adnivalis*. In the same year, Jeffrey (1986) retained the giant senecios in *Senecio*, and followed an alternative approach for *S. johnstonii* (discussed by Mabberley, 1973) by recognizing four geographic subspecies and twelve altitudinal varieties.

Jeffrey's (1992) acceptance of the segregate genus *Dendrosenecio* leaves us with the subgeneric classification of Mabberley (1973, 1986). Instead of reverting to Mabberley's classification in *Dendrosenecio*, or retaining Jeffrey's classification in *Senecio*, I offer below a provisional classification for *Dendrosenecio* for use in presenting my research results. This classification employs a synthetic approach similar to that defended by Nordenstam (1978) and Jeffrey (1979) and practiced by Mabberley (1973). Justification of this classification, along with any necessary refinement, will be presented in a full monographic treatment.

The Species of Giant Senecio from Eastern Africa

1. Dendrosenecio adnivalis (Stapf) E. B. Knox, comb. nov. *Senecio adnivalis* Stapf, J. Linn. Soc., Bot. 37: 521. 1906.

1a. Dendrosenecio adnivalis subsp. **adnivalis.**

1ai. Dendrosenecio adnivalis subsp. **adnivalis** var. **adnivalis.**
Distribution: Ruwenzori Mts., Zaire and Uganda.

1aii. Dendrosenecio adnivalis subsp. **adnivalis** var. **petiolatus** (Hedberg) E. B. Knox, comb. nov. *Senecio adnivalis* var. *petiolatus* Hedberg, Symb. Bot. Upsal. 15: 233. 1957.
Distribution: Ruwenzori Mts., Zaire and Uganda.

1b. Dendrosenecio adnivalis subsp. **friesiorum** (Mildbr.) E. B. Knox, comb. nov. *Senecio friesiorum* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 231. 1922.
Distribution: Ruwenzori Mts., Zaire.

2. Dendrosenecio battiscombei (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio battiscombei* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 1: 334. 1922.
Distribution: Aberdar es and Mt. Kenya, Kenya.

3. Dendrosenecio brassiciformis (R. E. Fr. & T. C. E. Fr.) Mabb. in F. Vuilleumier and M. Monasterio, High Altitude Tropical Biogeography, 100. 1986.
Distribution: Aberdares, Kenya.

4. Dendrosenecio cheranganiensis (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio cheranganiensis* Cotton & Blakelock, Bull. Misc. Inform. 1937: 364. 1937.

4a. Dendrosenecio cheranganiensis subsp. **cheranganiensis.**
Distribution: Cherangani Hills, Kenya.

4b. Dendrosenecio cheranganiensis subsp. **dalei** (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio dalei* Cotton & Blakelock, Bull. Misc. Inform. 1937: 365. 1937.
Distribution: Cherangani Hills, Kenya.

5. Dendrosenecio elgonensis (T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio elgonensis* T. C. E. Fr., Svensk Bot. Tidskr. 17: 229. 1923.

5a. Dendrosenecio elgonensis subsp. **elgonensis.**
Distribution: Mt. Elgon, Uganda and Kenya.

5b. Dendrosenecio elgonensis subsp. **barbatipes** (Hedberg) E. B. Knox, comb. nov. *Senecio barbatipes* Hedberg, Symb. Bot. Upsal. 15: 230. 1957.
Distribution: Mt. Elgon, Uganda and Kenya.

6. Dendrosenecio erici-rosenii (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Senecio erici-rosenii* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 330. 1922.

6a. Dendrosenecio erici-rosenii subsp. **erici-rosenii.**
Distribution: Mt. Muhi, Mt. Kahuzi, Virungas, and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

6b. Dendrosenecio erici-rosenii subsp. **alticola** (Mildbr.) E. B. Knox, comb. nov. *Senecio erici-rosenii* var. *alticola* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 230. 1922.
Distribution: Virungas, Zaire, Rwanda, and Uganda.

7. Dendrosenecio johnstonii (Oliv.) B. Nord., Opera Bot. 44: 42. 1978.
Distribution: Mt. Kilimanjaro, Tanzania.

8. Dendrosenecio keniensis (Baker f.) Mabb. in F. Vuilleumier and M. Monasterio, High Altitude Tropical Biogeography, 100. 1986.
Distribution: Mt. Kenya, Kenya.

9. Dendrosenecio keniodendron (R. E. Fr. & T. C. E. Fr.) B. Nord., Opera Bot. 44: 43. 1978.
Distribution: Aberdares and Mt. Kenya, Kenya.

10. Dendrosenecio kilimanjari (Mildbr.) E. B. Knox, comb. nov. *Senecio kilimanjari* Mildbr., Repert. Spec. Nov. Regni Veg. 18: 229. 1922.

10a. Dendrosenecio kilimanjari subsp. **kilimanjari.**
Distribution: Mt. Kilimanjaro, Tanzania.

10b. Dendrosenecio kilimanjari subsp. **cottonii** (Hutch. & G. Taylor) E. B. Knox, comb. nov. *Senecio cottonii* Hutch. & G. Taylor, Bull. Misc. Inform. 1930: 15. 1930.
Distribution: Mt. Kilimanjaro, Tanzania.

11. Dendrosenecio meruensis (Cotton & Blakelock) E. B. Knox, comb. nov. *Senecio meruensis* Cotton & Blakelock, Kew Bull. 2: 135. 1948.
Distribution: Mt. Meru, Tanzania.

THE GIANT LOBELIAS

The genus *Rhynchopetalum* was erected by Fresenius (1838; also 1839) to accommodate the discovery of the largest species of giant lobelia, the Ethiopian *R. montanum*, and was included the following year in the *Prodromus* by de Candolle (1839). This species was labeled by C. F. Hochstetter with the unpublished name *Tupa rhynchopetalum* in his distribution of W. G. Schimper's collections from Abyssinia. The genus *Tupa* had been recently described by Don (1834) for a group of Chilean species, and Richard (1850) published Hochstetter's name, along with his description of a second species, *T. schimperi*. A few years later, Ascherson (1869a, reported again in 1869b) presented another species, *T. deckenii* from Tanzania. Ascherson did not fully describe this species, but presented instead a table in which it was contrasted with *T. rhynchopetalum*. Vatke (1874) provided a more complete description when he illegitimately renamed this species *T. kerstenii*.

In *Genera Plantarum* (1873), Bentham submerged several allied genera into *Lobelia*. Section *Tupa* was restricted to the Chilean species, now known to be hexaploid (Lammers & Hensold 1992). Section *Rhynchopetalum* included African, Brazilian, Asian, and Pacific species now known to be tetraploid. Sections *Tylomium* and *Homochilus* also included robust (but not giant) tetraploid species, but each section contained at least one diploid species (Knox & Kowal, in press). Hemsley transferred the African species of giant lobelia to *Lobelia* in the *Flora of Tropical Africa* (1877). The names *L. montana* and *L. schimperi* were already in use for herbaceous species, and so *Rhynchopetalum montanum* (*Tupa rhynchopetalum*) was transferred as *L. rhynchopetalum*, and the Amharic vernacular was used to form *L. giberroa* for *Tupa schimperi*. As noted by Mabberley (1974b), *L. giberroa* was unfortunately presented in Hemsley's key, and later in *Index Kewensis*, as "*L. gibberoa*," an error that has been perpetuated (e.g., Baker 1898, 1908; De Wildeman 1922; Battiscombe 1926; Cotton 1944; Jex-Blake 1948; Dale & Greenway 1961; Coe 1967; Agnew 1974; Carlquist 1974). Schönland (1894) presented a broad concept of section *Tylomium* that included section *Rhynchopetalum*, an arrangement accepted by Fries and Fries (1922b) and Bruce (1934), but rejected by Hauman (1934). Fries and Fries, Bruce, and Hauman proposed various subsectional treatments to reflect the evolutionary relationships between the growing number of species described from eastern Africa.

Wimmer (1943, 1953, 1968) provided a treatment of Campanulaceae subfamily Lobelioideae for *Das Pflanzenreich*. Within the elevated subgenus *Tupa*, he restricted section *Rhynchopetalum* to species from eastern Africa, but excluded from this section one Tanzanian species, *Lobelia longisepala*. This he placed in section *Eutupa* subsection *Haynaldianae*, along with the Angolan *L. xongorolana*, the morphological sister-species of *L. stricklandiae*, which he retained in section *Rhynchopetalum*. The artificiality of Wimmer's classification was criticized by Mabberley (1974b) and is acknowledged by other workers (T. Ayers, T. Lammers, M. Thulin, pers. comm.).

Mabberley (1974b, 1975) retained Bentham's concept of section *Rhynchopetalum*, and proposed a subsectional treatment for the African species with suggestions concerning relationships with giant and herbaceous lobelias elsewhere in the

world. The most notable change with respect to specific treatment was his implementation (Mabberley 1974b) of Hedberg's (1957) suggestion that the six species of the *Deckenii* Group (Fries & Fries 1922b) be treated as subspecies. Thulin accepted this change in his treatment of Lobeliaceae for the *Flora of Tropical East Africa* (1984) and the *Flore d'Afrique Centrale* (1985), which are two parts of his regional treatment of this family (see also *Flora Zambesiaca*, 1983, and the *Flora of Ethiopia*, in press).

Since Thulin's treatment of the giant lobelias, three additional species from Tanzania have been recognized. *Lobelia morogoroensis* (Knox & Pócs 1992) had been previously collected as sterile material and was identified as *L. giberroa*. *Lobelia thuliniana* (proposed below; Fig. 2) had been previously collected as fertile material, but was identified variously as *L. giberroa* or *L. mildbraedii* (discussed in Knox, in press). The existence of the third new species, *L. ritabeaniana* (proposed below; Fig. 1), was predicted by Mabberley (1974b). During fieldwork in the Ukaguru Mountains, he discovered vegetative, but morphologically distinctive, plants (later named *L. sancta*; Thulin 1980), and he noted that "it is very likely that this or a similar species will be found on the upper slopes of the Nguru Mts., nearby."

In addition to the inclusion of new species, two other modifications of Thulin's treatment are made here. *Lobelia acrochila* has been elevated from varietal to species rank. This change was proposed in an unpublished manuscript by C. Puff in 1983, but Thulin (pers. comm.) considered the change unwarranted given the regional pattern of variation. Mabberley (1974b) treated *L. rhynchopetalum* var. *acrochilus* as a synonym of *L. rhynchopetalum* on the basis of the material available at the time, and his description of the variation reflects the fact that he was unable to inspect these plants in the field. In contrast, Thulin visited many of the sites that were accessible in the early 1980's and, with some reservation, felt that varietal treatment should be maintained. A specimen collected by J. Gillett (*Gillett 5317*) in 1933 from Gara Mulata, Harerge Region, that provided a distinctly intermediate combination of leaf and floral forms was considered of particular importance. This site has not been readily accessible, and the fieldwork needed to clarify the matter has not been conducted.

Some clarification was provided during a conversation with Mr. Gillett in 1989. Having promised to explain my reasons afterward, I asked him to recall any details concerning his collection of "a giant lobelia on Gara Mulata." After an initial disclaimer that memories fade with the passage of 56 years, he provided a very vivid and detailed account of the ascent, the vegetation, and his encounter with the giant lobelia. While describing the section of the inflorescence taken from a small plant growing on moist, flat ground, and the leaf taken from a "healthier" vegetative individual with the leaf-rosette borne on a well-developed trunk, growing among *Erica* shrubs on a nearby slope, Mr. Gillett interrupted himself with the conclusion that as a young botanist he had probably made a mixed collection. This anecdotal evidence provides insight into the origin of the most anomalous specimen. The prospect of peace in Ethiopia raises hope that the fieldwork needed to resolve this situation fully may be contemplated in the near future.

The final departure from Thulin's treatment is my classification of the *Lobelia deckenii* group. A conflict in the phylogenetic hypotheses suggested by morphology and chloroplast DNA evidence indicates a possible hybrid origin for *L. bequaertii* involving some ancestral member of the *L. deckenii* group and the

ancestor of the *L. wollastonii-L. stuhlmannii* species pair. The remaining members are classified as three species on the basis of comprehensive field studies. The three isolated (and formerly poorly known) populations of *L. burttii* are given subspecific rank to reflect the differentiation among them. Two altitudinal subspecies of *L. deckenii* on Mt. Kilimanjaro are recognized on the basis of ecological and morphological differentiation. The remaining members are treated as subspecies of *L. gregoriana*, the valid name for "*L. keniensis*" when treated at specific rank (Thulin 1983b).

The Species of Giant Lobelia from Eastern Africa

1. Lobelia aberdarica R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 403, figs. 5, 6a–d. 1922.
Distribution: Mt. Elgon, Cherangani Hills, Aberdares, and Mt. Kenya, Uganda and Kenya.

2. Lobelia acrochila (E. Wimm.) E. B. Knox, comb. nov. *Lobelia rhynchopetalum* var. *acrochilus* E. Wimmer, Ann. Naturhist. Mus. Wien 56: 368. 1948.
Distribution: Arsi, Bale, and Harerge Regions, Ethiopia.

3. Lobelia bambuseti R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 401, figs. 4, 6i–l. 1922.
Distribution: Aberdares and Mt. Kenya, Kenya.

4. Lobelia bequaertii De Wild., Rev. Zool. Africaines 8, Suppl. Bot.: 31. 1920.
Distribution: Ruwenzori Mts., Zaire and Uganda.

5. Lobelia burttii E. A. Bruce, Bull. Misc. Inform. 1933: 473. 1933.

5a. Lobelia burttii subsp. **burttii.**
Distribution: Mt. Hanang, Tanzania.

5b. Lobelia burttii subsp. **meruensis** E. B. Knox, subsp. nov.—Type: Tanzania, *Knox 1879* (holotype: MICH!; isotypes: BR! DSM! K! MO! UPS!).

Haec subspecies a *L. burttii* subsp. *burttii* internodiis elongatis, foliis grandibus, et corolla caeruleo-violacea differt.

Plant up to 2 m tall in flower, ascending or decumbent, suckering from the base with age to produce clumps of a few aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem 2–3 cm in diameter, terete, woody. Stem surface green, glabrous, developing with age a thin phelloderm. Terminal leaf rosette of 35–90 leaves, spirally arranged, deciduous, each leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-lanceolate, ca. 35 cm long, 3.5–5.0 cm wide, obtuse at the apex, tapering at the base, glabrous with a smooth, waxy cuticle on both surfaces; margin entire, ciliate; hydathodes embedded; terminal hydathode sometimes appearing mucronate; venation not prominent; midvein ca. 1.5 cm wide at the base; lateral veins 25–30 pairs, straight at 30–45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, ca. 30 cm long, ca. 2 cm in diameter at the base, borne atop a leafy peduncle 30–50 cm long, with little modification from mature vegetative leaves to

pedunculate leaves, and a sharp transition from pedunculate leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly 6.5–8.0 cm long, 2.4–3.2 cm wide, ovate; apex acute; base rounded, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, bracts, pedicels, hypanthia, and calyx lobes glabrous except bracts and calyx lobes ciliate. Pedicel 8–12 mm long, elongating only slightly during fruit maturation, with two linear bracteoles, 1 mm long, not opposite, crowded to one side, inserted one-half of the distance from the base. Hypanthium ovoid, 6–8 mm long, 9–10 mm wide, distinctly 10-nerved; extending beyond distal face of ovary to form a nectiferous cup. Calyx lobes 8–10 mm long, 5–6 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla 27–37 mm long, strongly downcurved at the base, bluish purple; inner surface densely pubescent with wide, curly trichomes in the throat, elsewhere glabrous; two lateral petals splitting along one-half of their length; three middle petals generally not splitting. Filaments ca. 22 mm long, connate except basal one-half, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla. Anther-tube 7–8 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; distal face yellow or orange. Capsule ovoid, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 2.2–2.3 mm long, compressed and frequently contorted, asymmetrically winged on both sides, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Meru, Tanzania.

5c. Lobelia burttii subsp. **telmaticola** E. B. Knox, subsp. nov.—TYPE: TANZANIA, *Knox 782* (holotype: MICH!; isotypes: DSM! K!).

Haec subspecies a *L. burttii* subsp. *burttii* caule crasso medulla lata, foliorum rosula robusta, inflorescentia grandi, et corolla longa differt.

Plant up to 2 m tall in flower, erect or ascending; with age, short rhizomes produce clumps of a few aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem ca. 6 cm in diameter, terete, woody. Stem surface obscured by densely packed leaf arrangement, developing with age a thin phelloderm. Terminal leaf rosette of 150–200 leaves, spirally arranged, deciduous, each leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-lanceolate, ca. 24 cm long, 2.7–3.0 cm wide, obtuse at the apex, phyllodic and slightly tapering at the base, glabrous with a smooth, waxy cuticle on both surfaces; margin entire, ciliate; hydathodes embedded; terminal hydathode appearing mucronate; venation not prominent; midvein ca. 1.0 cm wide at the base; lateral veins ca. 25 pairs, straight at 30–45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, ca. 100 cm long, ca. 4 cm in diameter at the base, borne atop a leafy peduncle 30–50 cm long, with little modification from mature vegetative leaves to pedunculate leaves, and a sharp transition from pedunculate leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly ca. 8.0 cm long, 3.5 cm wide, ovate; apex acuminate; base tapering, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, bracts, pedicels, hypanthia, and calyx lobes glabrous except bracts and calyx lobes ciliate. Pedicel 8–10 mm long, elongating only slightly during fruit maturation,

with two linear bracteoles, 1 mm long, not opposite, crowded to one side, inserted one-third of the distance from the base. Hypanthium obovoid, 11–13 mm long, 10–12 mm wide, distinctly 10-nerved; extending beyond distal face of ovary to form a nectiferous cup. Calyx lobes ca. 13 mm long, ca. 5 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla 33–42 mm long, strongly downcurved at the base, bluish purple; inner surface densely pubescent with wide, curly trichomes in the throat, elsewhere glabrous; two lateral petals splitting along one-half of their length; three middle petals generally not splitting. Filaments ca. 28 mm long, connate except basal one-half, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla. Anther-tube 8–10 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; color of distal face not known. Capsules ovoid, ca. 18 mm long, ca. 15 mm wide, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 1.9–2.2 mm long, compressed and frequently contorted, asymmetrically winged on both sides, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Loolmalassin, Tanzania.

6. Lobelia deckenii (Asch.) Hemsl., Fl. Trop. Afr. 3: 466. 1877.

6a. Lobelia deckenii subsp. **deckenii.**

Distribution: Mt. Kilimanjaro, Tanzania.

6b. Lobelia deckenii subsp. **incipiens** E. B. Knox, subsp. nov.—TYPE: TANZANIA, *Knox 2034* (holotype: MICH!; isotypes: BR! DSM! K! MO! UPS!).

Haec subspecies a *L. deckenii* subsp. *deckenii* caule gracili internodiis elongatis, foliis longis in rosula laxa, inflorescentia parva, et corolla alba differt.

Plant up to 2.5 m tall in flower, ascending, suckering profusely from the base with age to produce clumps of several aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Stem up to 3.7 cm in diameter, terete, woody. Stem surface green, glabrous, developing with age a thin phelloderm. Terminal leaf rosette of 40–80 leaves, spirally arranged, deciduous or weakly marcescent, each eventually leaving a conspicuous raised leaf scar. Leaves of mature non-flowering plant sessile, linear-oblanceolate, 29–36 cm long, 3.2–4.6 cm wide, acute or narrowly obtuse at the apex, tapering at the base, sparsely pubescent on both surfaces or sometimes glabrous; margin entire, ciliate; hydathodes embedded; terminal hydathode prominent; venation prominent below; midvein 2–3 mm wide at the base; lateral veins 40–45 pairs, straight at 45° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 30–45 cm long, ca. 3 cm in diameter at the base, borne atop a leafy peduncle 20–40 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Bracts uniformly 6.5–8.0 cm long, 2.5–2.7 cm wide, lanceolate; apex acuminate; base rounded, decurrent; margin nearly entire with small, embedded hydathodes; mucronate. Rachis, pedicels, and hypanthia glabrous. Bracts sparsely ciliate, glabrous or with sparse pubescence along the midvein on the upper surface; calyx lobes sparsely ciliate but otherwise glabrous. Pedicel 6–7 mm long,

elongating to 10–13 mm during fruit maturation; with two fleshy bracteoles, 2 mm long, subopposite, crowded to one side, inserted one-quarter of the distance from the base. Hypanthium campanulate, 5–7 mm long, 10–12 mm wide, distinctly 10-nerved, not forming a nectiferous cup. Calyx lobes 7–12 mm long, 4–5 mm wide, subulate, obtuse at the apex, mucronate; margin nearly entire; lower two lobes shorter than the upper three. Corolla ca. 36 mm long, not strongly downcurved except at the tip, white, glabrous; petals generally not splitting, but slits between petals not uncommon. Filaments ca. 30 mm long, connate except basal one-third, forming a firm tube, glabrous; free sections of filaments with parallel margins, except widely flaring at the base to become connate at the point of attachment with the hypanthium and corolla; scattered pubescence on inner surface. Anther-tube ca. 10 mm long, glabrous except the two lower anthers barbate at the apex; bristles 2 mm long. Ovary inferior; distal face yellow. Capsule globose, 15–16 mm long, 12–14 mm wide, 10-nerved, glabrous, with two distinct valves. Bracts and calyx lobes retained; all other floral parts marcescent. Seeds transversely ovate to reniform in outline, 1.8–2.0 mm long, compressed and frequently contorted, asymmetrically winged on one side, finely striate, brown with a cream-colored wing, becoming orange-brown with age. Seedling a compact rosette.

Distribution: Mt. Kilimanjaro, Tanzania.

7. Lobelia giberroa Hemsl., Fl. Trop. Afr. 3: 465. 1877.
Distribution: Ethiopia to Malawi, inland to Zaire.

8. Lobelia gregoriana Baker f., J. Bot. 32: 66. 1894.

8a. Lobelia gregoriana subsp. **gregoriana.**
Distribution: Mt. Kenya, Kenya.

8b. Lobelia gregoriana subsp. **sattimae** (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Lobelia sattimae* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 414. 1922.
Distribution: Aberdare Mts., Kenya.

8c. Lobelia gregoriana subsp. **elgonensis** (R. E. Fr. & T. C. E. Fr.) E. B. Knox, comb. nov. *Lobelia elgonensis* R. E. Fr. & T. C. E. Fr., Svensk Bot. Tidskr. 16: 411, fig. 7a. 1922.
Distribution: Mt. Elgon and Cherangani Hills, Uganda and Kenya.

9. Lobelia longisepala Engl., Bot. Jahrb. Syst. 32: 117. 1902.
Distribution: Usambara Mts., Nguru Mts., Uluguru Mts., Uzungwa Mts., Mahenge Highlands, Tanzania.

10. Lobelia lukwangulensis Engl., Notizbl. Königl. Bot. Gart. Berlin 1: 107. 1895.
Distribution: Uluguru Mts. and Uzungwa Mts., Tanzania.

11. Lobelia mildbraedii Engl. in J. Mildbraed, Wiss. Erg. deut. Zentr.-Afr. Exped., Bot., 344. 1914.
Distribution: Several sites, disjunct between northern Malawi/southernTanzania and Zaire, Burundi, Rwanda, and Uganda.

12. Lobelia morogoroensis E. B. Knox & Pócs, Kew Bull. 47: 505. 1992.
Distribution: Morogoro Region, Tanzania.

13. Lobelia petiolata Hauman, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8°) 2: 36, fig. 5. 1934.
Distribution: Mts. Kahuzi and Biega, Zaire and Nyungwe Forest, Rwanda.

14. Lobelia rhynchopetalum Hemsl., Fl. Trop. Afr. 3: 465. 1877.
Distribution: Gondar, Gojam, Shewa, Arsi, Bale, and Harerge Regions, Ethiopia.

15. Lobelia ritabeaniana E. B. Knox, sp. nov.—TYPE: TANZANIA, *Pócs & Mankte-low 91426* (holotype: UPS!; isotypes: BP! K! MICH! NHT!). Fig. 1.

Haec species a *L. sancta* inflorescentia non ramosa, bracteis angustis integrisque, et antheris thecis glabris differt.

Plants up to 4 m tall in flower, erect or ascending, not suckering from the base, not branching vegetatively; with an unbranched inflorescence. Stem 3–5 cm in diameter at the base, terete, woody. Stem surface green, glabrous, developing with age a thin phelloderm. Pith 1–2 mm in diameter at the base, 15–25 mm in diameter and hollow above. Terminal leaf rosette of 60–200 leaves, spirally arranged, deciduous, each with a conspicuous raised leaf-scar with a corky abscision layer. Leaves of mature non-flowering plant subsessile, narrowly oblanceolate, 25–40 cm long, 2–3 cm wide, acuminate at the apex, attenuate at the base, glabrous on both surfaces with a smooth, waxy cuticle prominent on the upper surface; margin often somewhat revolute, weakly or coarsely dentate with teeth up to 5 mm wide and 3 mm long, often appearing doubly dentate due to prominent hydathodes; terminal hydathode appearing mucronate; venation prominent beneath; midvein 2–3 mm wide at the base; lateral veins 25–30 pairs, arcuate at 60–90° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 50–100 cm long, 1–2 cm in diameter at the base, borne atop a leafy peduncle 55–150 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Lowermost bracts 30–35 mm long, 5–8 mm wide, with successive bracts more uniformly 25–30 mm long, 3–4 mm wide; margin entire or papillose; mucronate. Rachis, pedicels, and hypanthia sparsely puberulent or papillose. Pedicel 6–8 mm long, not elongating during fruit maturation, ebracteolate. Hypanthium campanulate, 6–7 mm long, 7–8 mm wide, distinctly 10-nerved; not forming a nectiferous cup. Calyx lobes uniformly 19–20 mm long, ca. 3 mm wide, subulate, glabrous; margin entire or papillose; mucronate. Corolla 40–44 mm long, strongly downcurved in the middle, pink to magenta; inner surface densely papillose along the throat, sparser toward the base, glabrous elsewhere; petal margin generally entire, with scattered papillae or longer trichomes, particularly at the tip; two lateral petals splitting along half their length, and also split up to 9 mm from the base; three middle petals split less than half their length. Filaments ca. 28 mm long, connate except basal 1 mm, forming a firm tube, flaring evenly toward the base; outer surface puberulent or papillose, particularly the basal portion of the lower two anthers. Anther-tube ca. 6 mm long, trichomes frequently found in small tufts along sutures at the base of the anthers, the two lower anthers barbate at the apex; bristles 1 mm long. Ovary subinferior; distal face not brightly colored. Capsule subglobose, 10–12 mm long, 8–10 mm wide, 10-nerved, puberu-

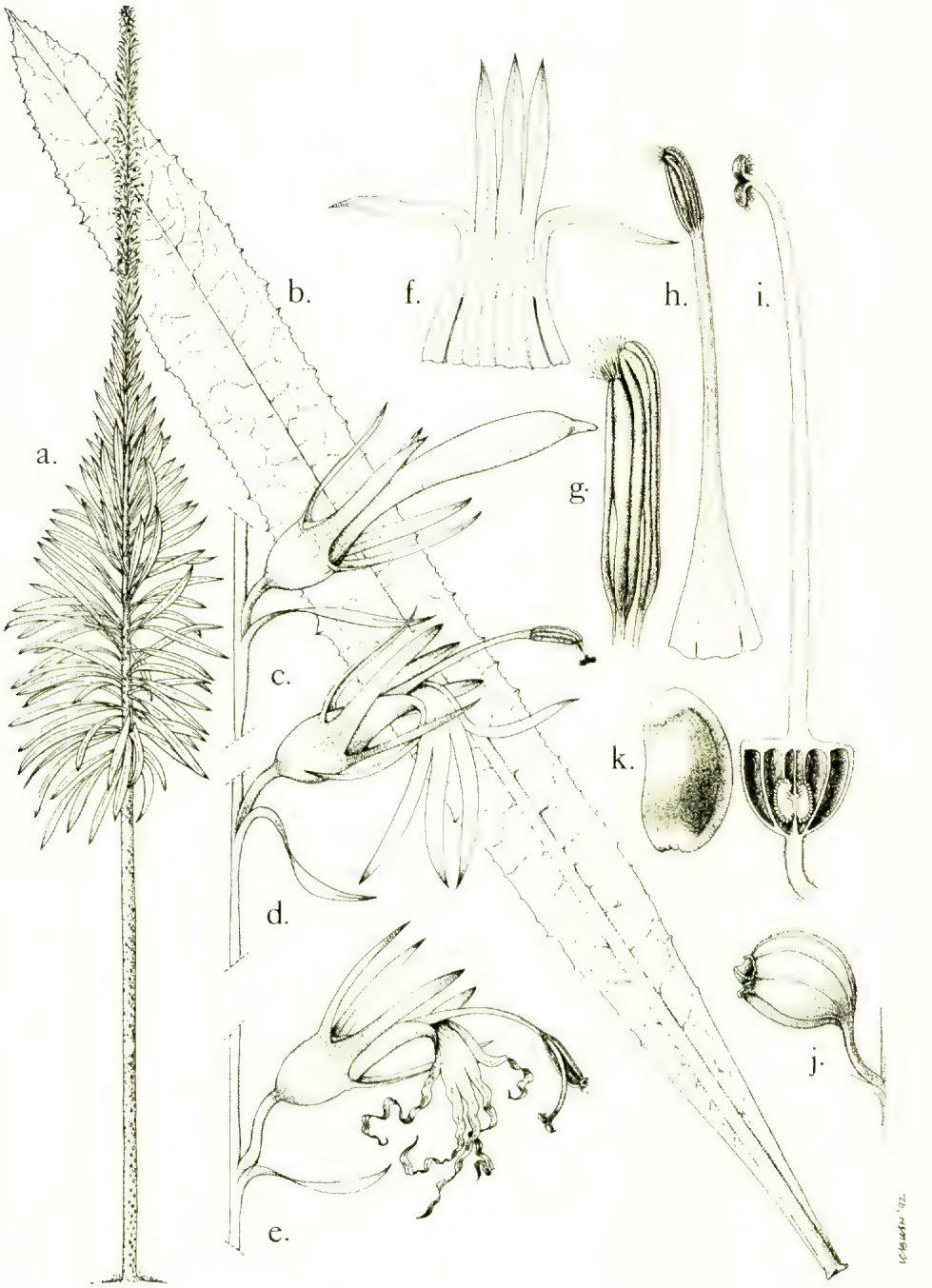

FIG. 1. *Lobelia ritabeaniana*. A. Habit, ×0.04. B. Leaf, ×0.5. C. Flower in bud, ×1. D. Flower in female phase (male phase not shown), ×1. E. Early stage of fruit development, ×1. F. Corolla spread out, ×1. G. Stamens (side view), ×2. H. Anther-tube, ×6. I. Ovary and style from female phase flower, ×1.5. J. Mature fruit, ×1.5. K. Seed, ×20. Drawn by L. Bush.

lent, with two distinct valves. Bracts retained; calyx lobes frequently lost during fruit maturation; all other flower parts deciduous. Seed irregularly ovate in outline, ca. 1.1 mm long, somewhat compressed, lipped on one side, finely striate, dark brown with cream-colored margin. Seedlings found growing in shade with

slender stems, 3–4 mm in diameter, internodes 4–5 mm long, and leaves almost spathulate; in full light the growth-form is more robust with a wide hollow stem quickly produced and leaves characteristically oblanceolate.

Distribution: Nguru Mts., Tanzania.

16. Lobelia sancta Thulin, Kew Bull. 34: 815, fig. 1. 1980.
Distribution: Ukaguru Mts., Tanzania.

17. Lobelia stricklandiae Gilliland, J. Bot. 73: 248, as "stricklandae." 1935.
Distribution: Several sites, Tanzania to NE Transvaal.

18. Lobelia stuhlmannii Stuhlmann, Mit Emin Pascha ins Herz von Afrika, 291, 295, and 300, excl. fig. 11. 1894.
Distribution: Mt. Muhi, Mt. Kahuzi, Virungas, and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

19. Lobelia telekii Schweinf. in L. von Höhnel, Zum Rudolph- und Stephanie-See, 861, fig. 104. 1892.
Distribution: Mt. Elgon, Aberdares, and Mt. Kenya, Uganda and Kenya.

20. Lobelia thuliniana E. B. Knox, sp. nov.—TYPE: TANZANIA, *Knox & Butler 2256* (holotype: MICH!; isotypes: DSM! EA! K! MO! UPS!). Fig. 2.

Haec species a *L. giberroa* rhizomate brevi, caule gracili et fere herbaceo, folio breviore, angustiore et fere petiolato, insertione basali bracteolarum, et trichomatibus setaceis secus longitudinem 2 antherarum infernarum differt.

Plant up to 3 m tall in flower, erect; with age in favorable habitats, numerous short rhizomes produce dense stands of aerial stems, but not otherwise branching vegetatively; with an unbranched inflorescence. Rhizome 1–2 cm in diameter, rooting adventitiously, with pith 0.5–1.0 cm in diameter, surrounded by wood 3–5 mm thick. Aerial stem 2–3 cm in diameter throughout its length, terete, hollow or with occasional light pith. Stem surface green, glabrous, developing with age a thin phelloderm. Terminal leaf rosette of 30–80 leaves, spirally arranged, marcescent; lower leaves eventually deciduous, each leaving a small, raised leaf scar with a corky abscission layer. Leaves of mature non-flowering plant subsessile, oblanceolate, 25–45 cm long, 2.5–4.0 cm wide, acute at the apex, attenuate at the base; upper surface nearly glabrous with a smooth waxy cuticle and sparse, short pubescence; lower surface pubescent primarily along veins; margin finely serrulate due to prominent hydathodes; terminal hydathode appearing mucronate; venation prominent beneath; midvein 2–3 mm wide at base; lateral veins 15–25 pairs, mostly arcuate at 45–60° to the midvein. Inflorescence a dense, cylindrical, hollow raceme, 50–80 cm long, 1–2 cm in diameter at the base, borne atop a leafy peduncle ca. 40 cm long, with a transition from mature vegetative leaves to the nearly uniform bracts that subtend each flower. Lowermost bracts 45–65 mm long, 3–6 mm wide, with successive bracts more uniformly 27–48 mm long, 2–4 mm wide; margin entire; minutely mucronate. Peduncle, rachis, bracts, pedicels, hypanthia, and calyx lobes puberulent, pubescent, or tomentose. Pedicel 5–12 cm long, elongating only slightly during fruit maturation, with two subulate, pubescent bracteoles, 1 mm long, subopposite, inserted at the base. Hypanthium campanulate, 5–7 mm long, 6–8 mm wide, indistinctly 10-nerved; not forming a nectiferous cup. Calyx

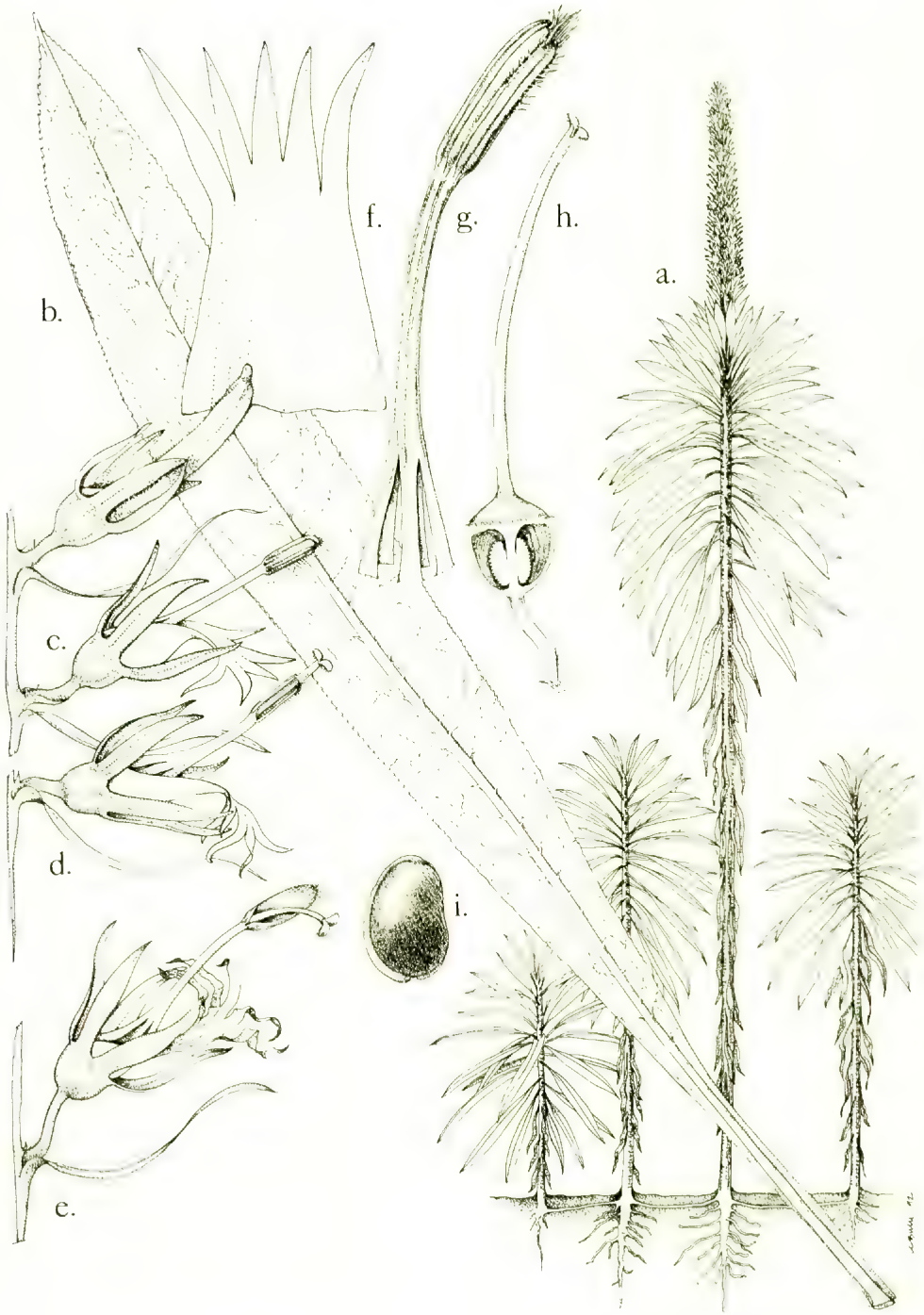

FIG. 2. *Lobelia thuliniana*. A. Habit, ×0.05. B. Leaf, ×0.5. C. Flowers in bud and male phase, ×1. D. Flower in female phase, ×1. E. Mature fruit, ×1. F. Corolla spread out, ×1.5. G. Stamens (side view), ×2. H. Ovary and style from female phase flower, ×1.5. I. Seed, ×20. Drawn by L. Bush.

lobes uniformly 15–20 mm long, ca. 3 mm wide, subulate; margin entire; mucronate. Corolla 28–35 mm long, not strongly downcurved, white or greenish; inner surface glabrous; outer surface densely pubescent distally, more sparse toward the base; two lateral petals generally splitting along half their length; three middle petals generally splitting less than a third of their length, but the pattern of splitting is variable. Filaments ca. 25 mm long, connate except basal one-third, forming a firm tube, glabrous; free sections of filaments with parallel margins, only slightly flaring and not becoming connate at the point of attachment with the hypanthium and corolla. Anther-tube ca. 10 mm long, the two lower anthers barbate at the apex, bristles extending along connectives and frequently found on the apices of the three upper anthers; bristles 1–2 mm long. Ovary subinferior; distal face yellow. Capsule subglobose, 10–11 mm long, 8–10 mm wide, 10-nerved, glabrescent, with two distinct valves. Seeds ovate in outline, ca. 0.8 mm long, somewhat compressed, slightly lipped on one side, finely striate, orange-brown. Seedling initially compact but rapidly developing an erect stem.

Distribution: Iringa Region, Tanzania.

21. Lobelia wollastonii Baker f., J. Linn. Soc., Bot. 38: 265, pl. 19, fig. 7. 1908.

Distribution: Virungas and Ruwenzori Mts., Zaire, Rwanda, and Uganda.

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A NEW SPECIES OF HORNSCHUCHIA (ANNONACEAE) FROM ATLANTIC BRAZIL, WITH COMMENTS ON THE CIRCUMSCRIPTION OF THE GENUS TRIGYNAEA

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Hornschuchia Nees is endemic to the Atlantic Coast forests of eastern Brazil. Its small flowers with only six stamens and 3–5 carpels are atypical in the Annonaceae. In fact, *Hornschuchia* was assigned to the Sapindaceae, Sapotaceae, Olacaceae, Ebenaceae, Lardizabalaceae, Menispermaceae, and Styracaceae before its affinity to Annonaceae was finally recognized (Fries 1931).

Previously the only fruit type known in *Hornschuchia* was an aggregate of 1–3 linear thin-walled monocarps with several terete seeds attached laterally and inclined obliquely to the long axis of the monocarp. Recent collecting in Brazil has yielded a plant with the long-conic flower buds and connate sepals typical of a *Hornschuchia*, but which has an ovoid thick-walled monocarp with trigonous seeds that are perpendicular to the long axis, a fruit and seed morphology more like those found in the related genus *Trigynaea* Schlechtendal. We provide a description of this distinctive species here, followed by a discussion of its proper generic placement.

Hornschuchia citriodora D. M. Johnson, sp. nov.—TYPE: BRAZIL. Espírito Santo: Guarapari, Rodovia do Sol, estrada que liga a BR-101 à Praia Setiba na ES-060 a 6 km da BR-101, 40°27'W, 20°33'S, 23 Feb 1988 (fl! fr!) *Pirani et al. 2435* (holotype: SPF-2 sheets!; isotypes: MBM! NY-2 sheets! OWU-2 sheets! RB! U!). Fig. 1.

Species floribus grandibus solitariis, pedicellis 8.5–11.5 mm longis ex internodiis dependentibus, carpellis numero 3–5 variantibus, monocarpiis ovoideis, et seminibus oblongo-ellipsoideis subangulatis intra monocarpium transverse dispositis congeneribus differt.

Treelet 5 m tall, DBH 5–6 cm. Leaf-bearing twigs 1–3 mm thick, dark brown to pale gray, glabrate. Lamina of larger leaves 13.5–18.6 cm long, 4.8–7.0 cm wide, chartaceous to subcoriaceous, elliptic to oblong–elliptic; base narrowly to broadly cuneate; apex short-acuminate, the tip 11–15 mm long; surface glabrous; midrib plane or slightly impressed adaxially, raised abaxially; secondary veins 8–10 per side, at 50–70° to midrib, slightly raised adaxially, more strongly so abaxially; higher-order veins slightly raised on both surfaces. Petiole 5–6 mm long, 1.5–2.1 mm

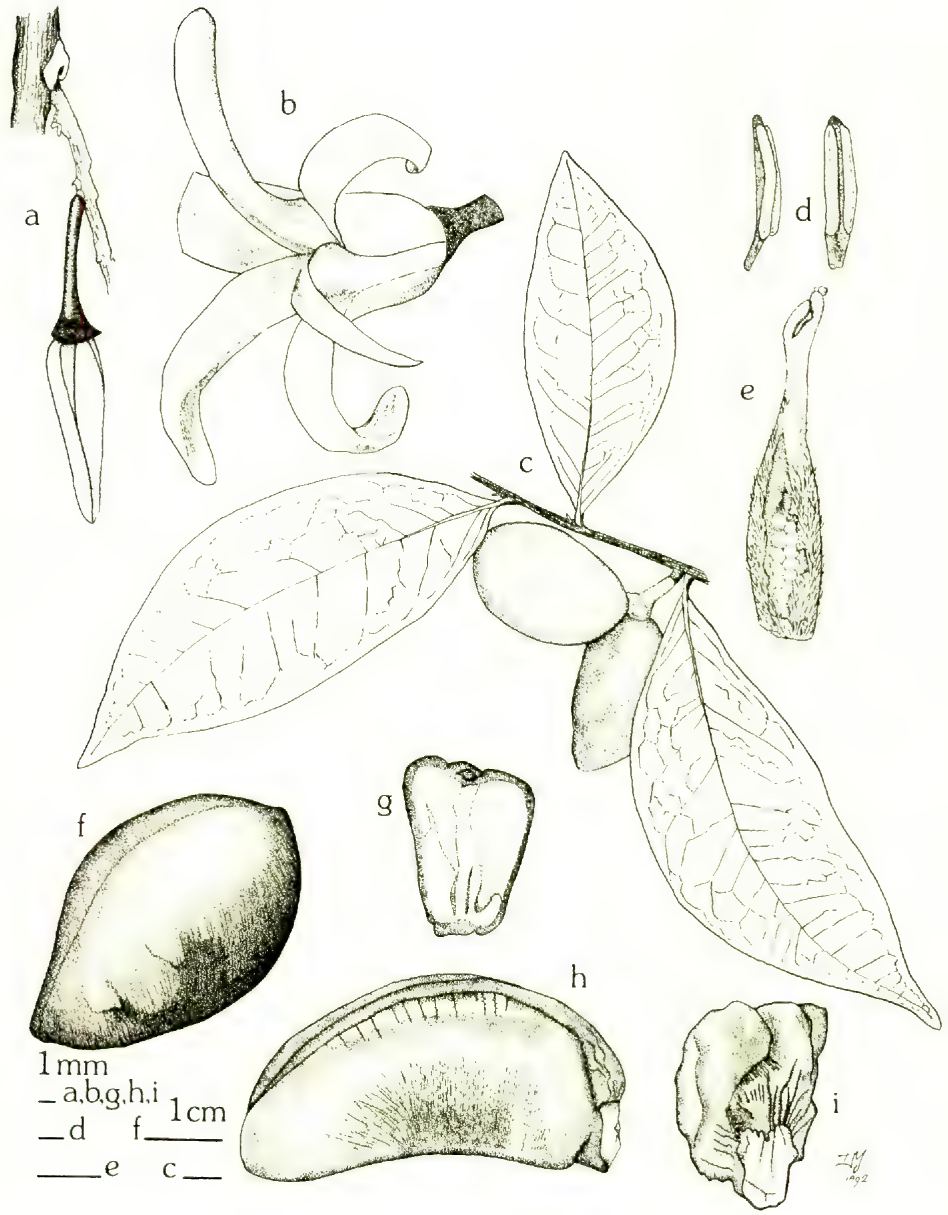

FIG. 1. *Hornschuchia citriodora*. a, flower bud; b, flower at anthesis; c, habit; d, stamens, lateral view on left and dorsal view on right; e, carpel with portion of ovary wall removed to show ovules; f, monocarp; g, seed in cross section, showing the platelike ruminations of the seed coat into the endosperm; h, seed, lateral view; i, seed, end view showing hilar region. (a, d, e based on *Pirani et al. 2435*; b, c, f–i based on *Johnson et al. 1848*.)

wide. Flowers solitary, the pedicel internodal or supra–axillary, or less commonly compound and axillary, 8.5–11.5 mm long, 0.5–1 mm thick at midpoint in flower. Buds long-conic, acute at apex. Calyx 3.1–3.5 mm in diameter, 1.5 mm deep, discoid, the lobes apiculate, sparsely pubescent along margins on both surfaces. Corolla white, petals revolute at anthesis. Outer petals 12–14.7 mm long (30 mm long in flower preserved in ethanol), 1.9–2.3 mm wide, lanceolate-ligulate, flat or with a slight keel adaxially, acute at apex, glabrous adaxially, pubescent along

midrib and margins abaxially; inner petals 11–12 mm long (35 mm long in flower preserved in ethanol), 2.5 mm wide, linear-lanceolate, increasingly concave adaxially from about midpoint to the base, puberulent in concavity, otherwise glabrous. Stamens 6, 4.5 mm long, oblong, connectives obtuse at the apex. Carpels 3–5; ovary 4 mm long, pubescent; ovules 9–12, in two rows on adaxial wall of ovary; stigmas ca. 1.0 mm long, globose to clavate. Torus in flower 1.5 mm in diameter, flat to slightly convex, hispid. Pedicel in fruit 10 mm long, 2.2 mm wide, longitudinally wrinkled; torus in fruit 4 mm in diameter; calyx persistent in fruit. Monocarps 4.3 cm long, 2.6–2.8 cm wide; ovoid, sessile, glabrous, shiny (in vivo); base rounded; apex bluntly conical; wall rugulose and 1 mm thick when dry. Seeds ca.8, at 90° to long axis of monocarp, 15–19 mm long, 8.5–9.5 mm wide, irregularly oblong–ellipsoid, subangulate in cross section, brown (tan in vivo); caruncle absent; hilum 3.5 mm long, 1.5 mm wide.

Additional Specimens Examined. **Brazil**. Bahia: Mpio. Alcobaça, Km 6–8 da Rod. BA 001, trecho Alcobaça/Caravelas, 16 Sep 1978 (fl), *Santos et al. 3328* (CEPEC).—Espírito Santo: along rd connecting BR-101 and ES-060 (marked as rd for Praia do Sol), 6 km from BR-101, 3 km from ES-060 [=type locality], 31 Jul 1991 (fl, fr), *Johnson et al. 1848* (CEPEC, NY, OWU).

Hornschuchia citriodora is distinctive within its genus by the combination of sharply pointed flower buds, 3–5 carpels per flower, and ovoid monocarps with transversely arranged trigonous seeds. In its flowers that are borne singly on the internodes of leafy branches it may be distinguished from *H. bryotrophe* Nees, *H. polyantha* P. Maas, *H. cauliflora* P. Maas & van Setten, and *H. obliqua* P. Maas & van Setten, all of which have multiple flowers borne either on the trunk or on specialized leafless inflorescence branches. The other species with solitary internodal flowers, *H. myrtillus* Nees and *H. alba* (St. Hilaire) R. E. Fries, both have much smaller leaves (maximum length 8 cm); in addition, the flower pedicels of *H. myrtillus* are 10–15 mm long and more slender, and in *H. alba* the calyx is pubescent and deeply cup-shaped (2 mm deep).

This species is known at present from only two localities, one in southern Bahia and the other in Espírito Santo, in wet forest near sea level. This distribution straddles an important phytogeographic line on the Brazilian coast. North of the Rio Doce the minimum temperature is never lower than 18°C and the higher rainfall (ca. 1300 mm annually, is evenly distributed throughout the year. South of the river the temperatures can be lower, the rainfall is more seasonal, and the total annual precipitation is lower as well (Soderstrom & Calderón 1974).

Only a single individual of this species was found at the Espírito Santo locality in a forest remnant with species such as *Esenbeckia grandiflora* Mart. (Rutaceae), an undescribed species of *Galipea* (Rutaceae), *Hornschuchia bryotrophe*, *Phyllostemonodaphne geminiflora* (Meissn.) Kosterm. (Moraceae), *Ravenia infelix* Vell. (Rutaceae), and *Sorocea hilarii* Gaud. (Moraceae), as well as species of *Aspidosperma* (Apocynaceae), *Bathysa* (Rubiaceae), *Bauhinia* (Caesalpiniaceae), *Cordia* (Boraginaceae), *Dichorisandra* (Commelinaceae), *Eschweilera* (Lecythidaceae), *Jacaratia* (Caricaceae), *Lygodium* (Schizaeaceae), *Mollinedia* (Monimiaceae), *Ouratea* (Ochnaceae), *Passiflora* (Passifloraceae), *Paullinia* (Sapindaceae), *Piper* (Piperaceae, two species), *Rinorea* (Violaceae), and *Senna* (Caesalpiniaceae). A flower at anthesis on a cut branch produced at dusk a strong fragrance of *Citrus* flowers, but no flower visitors were observed in the field.

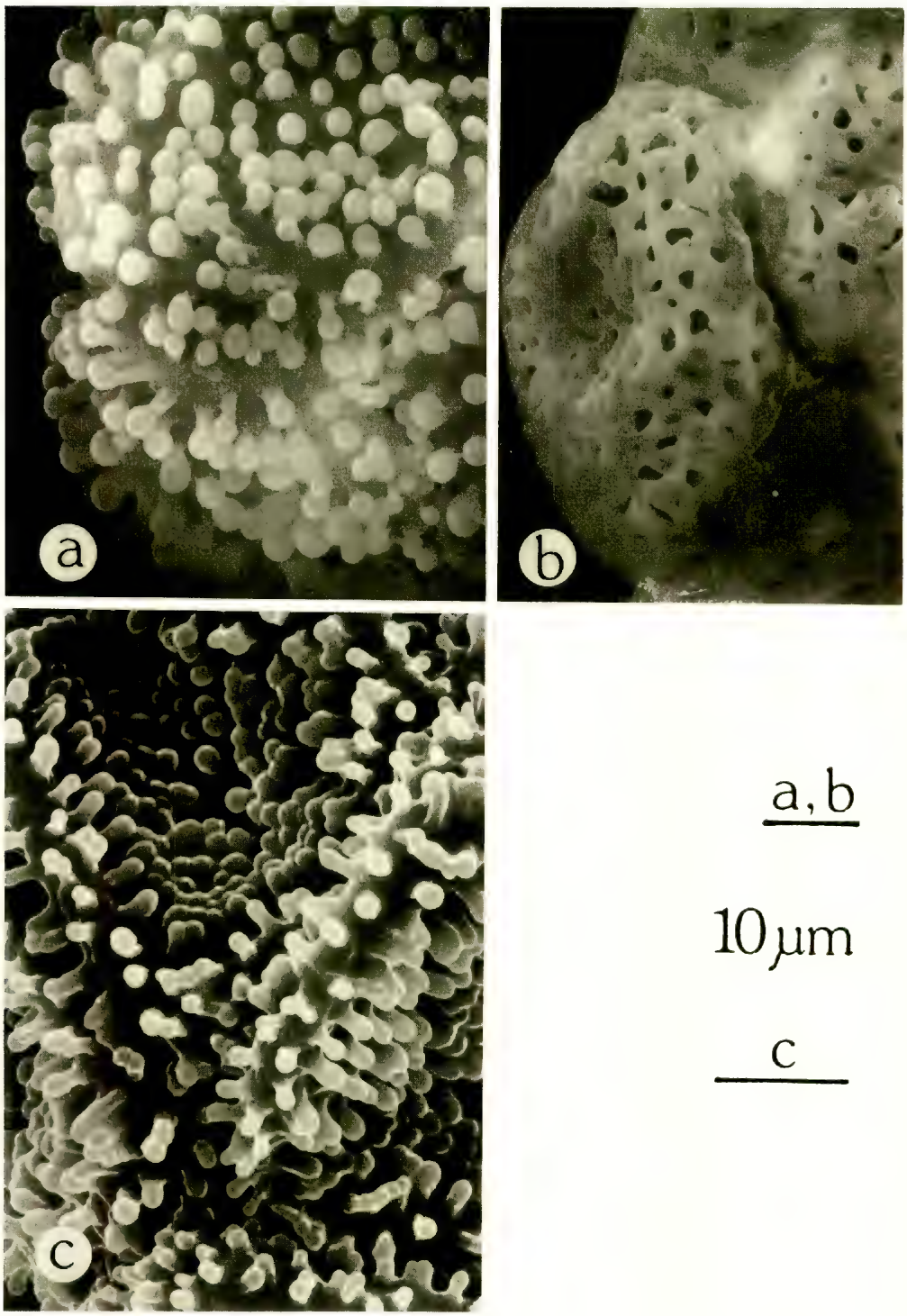

FIG. 2. SEM photographs of surface ornamentation of pollen grains. Only a portion of the entire octad is shown for each species. a, *Hornschuchia citriodora* (*Pirani et al. 2435*), with club-shaped columellae on the surfaces of three grains; b, *H. bryotrophe* (*Johnson et al. 1847*), showing the perforate tectum formed by fusion of the apices of hidden columellae on the surfaces of four grains; c, *Trigynaea* aff. *duckei* (R. E. Fries) R. E. Fries (*Foster 9212*), with rod-shaped columellae on the surfaces of four grains.

Fries (1959, recognized three genera within his "Trigynaea Gruppe" that have small flowers and apiculate anther connectives: *Trigynaea* Schlechtendal, *Bocagea* St. Hilaire, and *Hornschuchia*. He distinguished *Trigynaea* from *Hornschuchia* on the basis of its numerous (24 or more) versus only six stamens, plus the free sepals of the former versus the connate sepals of the latter. He also described *Trigynaea* as having rounded flower buds, 1–6 ovoid carpels, and a rounded or obovate monocarp, whereas *Hornschuchia* had elongate-cylindric flower buds, 3 linear-oblong carpels, and narrowly ellipsoid or spindle-shaped monocarps.

A further difference between the two genera was reported by Walker (1971), who found pollen with tectate-columellate exine in polyads of 16 grains in *Hornschuchia bryotrophe*, but intectate-columellate exine and polyads of 8 grains in the pollen of the three species of *Trigynaea* he sampled (Fig. 2). The intectate exine pattern is highly restricted within the Annonaceae, previously known elsewhere only in the African genus *Ophrypetalum* Diels (Walker 1972), which has pollen in tetragonal tetrads. *Hornschuchia citriodora* and several other species of *Hornschuchia* are now known to have intectate-columellate pollen in octads as well.

The generic boundaries between *Hornschuchia* and *Trigynaea* are therefore blurred. Like other species of *Hornschuchia*, *H. citriodora* has long-conic buds, connate sepals, linear-oblong carpels, and only six stamens. With *Trigynaea* it shares the characters of 3–5 carpels, ovoid monocarps, and trigonous seeds. Tectate versus intectate pollen no longer provides a generic distinction. Should *Hornschuchia* and *Trigynaea* be combined, the name *Hornschuchia*, the older of the two, will stand.

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RESUMO

É descrita e ilustrada uma nova espécie de Annonaceae, *Hornschuchia citriodora,* da flora costeira do leste sudeste do Brasil. A nova espécie conquanto possua características típicas de *Hornschuchia* como o formato dos botões florais, das sepalas, dos carpelos e número de estames, compartilha com o gênero afim, *Trigynaea,* caracteres como o pólen, o número de carpelos e o formato dos carpídios e sementes, tornando questionável a distinção destes gêneros.

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QUANTIFICATION OF THE CONTRIBUTION TO THE CONSERVATION OF BIOLOGICAL DIVERSITY AS A GUIDE TO THE MANAGEMENT OF NATURE RESERVES, WITH APPLICATION TO THE RISERVA NATURALE DI MONTE RUFENO, LAZIO, ITALY

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INTRODUCTION

The general interest to conserve nature has led to the establishment and protection of nature reserves. Public awareness of the importance of these reserves for the protection of biological diversity in the interest of present and future human welfare is increasing. Also increasing are economic pressures to destroy nature by consumption, development, and pollution. Decisions to establish public lands (national/regional forests, parks, wetlands, shorelines, wildlife refuges, etc.), and to manage them in various ways, are thus the consequence of considerations of both human politics and natural science. To contribute to this decision process, natural scientists can develop objective, quantitative methods to define and measure the natural values to be protected in reserves, and can suggest appropriate management technology for protecting them.

It would be useful to the decision process for establishing and managing nature reserves to know the contribution that each of several related actual or potential nature reserves, or that each of the several geographical areas actually or potentially constituting a single nature reserve, would make to the effectiveness of the whole for the conservation of biological diversity. Here we present some concepts for quantifying the contribution that each of several areas constituting a nature reserve makes to the effectiveness of the entire nature reserve for preserving biological diversity. Biological diversity can be measured with respect to individual species, vegetation, habitats, biogeographical regions, or any other conceptual entity whose variety is to be protected. To illustrate these concepts we present data on vegetation types occurring in various geographical areas constituting the Riserva Naturale di Monte Rufeno in Lazio, Italy.

DIVERSITY CONTRIBUTION

Consider a nature reserve composed of several geographical areas each containing various amounts of the various kinds of the natural entities that the nature reserve would conserve. In the application to follow, these entities are vegetation types and their amounts are expressed in hectares. In other applications for example, the entities might be species (or other taxonomic or biogeographical unit) and the amounts might be individuals.

One useful concept of the diversity of entities in the reserve might be the number (richness) of distinct entities found there. This concept fails to take into account the relative amounts of the various conserved entities. Simpson's diversity index can be used to take this into account. It is calculated as the reciprocal of the sum of the squared fractions of the total amount that is represented by each entity in the reserve. If all the entities present are represented by equal amounts, then Simpson's diversity index has the same value as richness. If these amounts are not all equal, then Simpson's diversity index has a value lower than richness. Richness and Simpson's diversity index can also be calculated for each of the several areas constituting the reserve.

We wish to ask how much does an individual area, with the various amounts of its various entities, contribute to the diversity of entities conserved by the whole reserve. We answer this by imagining that this individual area has been omitted from the reserve, and then recalculating the diversity measure for the reserve as it would be without this area. The difference, diversity of original reserve including this area minus diversity of the reserve without this area, is the contribution to the diversity of the reserve made by this particular area. In this way, the contribution of each area to the diversity conserved by the reserve can be calculated.

A large reserve may be considered more effective for conserving natural diversity than a small one. In addition to conserving more of the entities of interest, a larger size may better enable important natural dynamic processes (pollination, dispersal, establishment, mortality, outcrossing, animal activity, etc.) to occur. Diversity of a reserve does not explicitly reflect it's size. One way to represent both its size and its diversity is to multiply its diversity by the total amount of the entities in it. This quantifies diversity-amount. Each area in a reserve makes a contribution to the diversity-amount of the reserve. This contribution can be determined in the same way as was determined its contribution to the diversity of the reserve: remove the area from the reserve; recalculate the reserve's diversity-amount without this area; and subtract this diversity-amount from the diversity-amount of the reserve including this area. The diversity-amount of an individual area can be easily calculated as the product of it's diversity times the amount of the entities conserved in it.

By virtue of conserving a larger amount of entities, larger areas can potentially contribute more to a reserve's diversity-amount than can smaller areas. We can calculate the efficiency with which an area, large or small, uses the amount of entities it conserves to contribute to the reserve's diversity-amount. To do this, we divide an area's contribution to the reserve's diversity-amount by that area's amount. The efficiency of an area is comparable to its diversity. If the amount conserved in an area contributes as efficiently to the reserve's diversity amount as it does to it's own, then its efficiency would equal its diversity. An area with efficiency higher than its diversity makes an additional contribution.

RISERVA NATURALE DI MONTE RUFENO

The Riserva Naturale di Monte Rufeno, established in 1983, is one of several parks and nature reserves of the region of Lazio in Italy. It is located in the northernmost sector of Lazio near the border with the regions of Toscana and Umbria, between the mountain range Monti Vulsini on one side and the mountain Monte Amiata on the other. Its approximately three thousand hectares are spread out over hills covered with copious woodland. The vegetation is composed mostly of various oaks, but there are also mediterranean scrub as well as pine woods planted thirty years ago on abandoned farmland, among other less abundant types.

The reserve is surrounded with a buffer-zone. Within the reserve, areas are designated for management in accordance with one of three purposes; a) strict conservation of the natural entities present; b) restoration and preservation of the natural ecosystem in conjunction with compatible human economic activity; c) human recreational activity, with some protection for the environmental aesthetics that support it. Nine geographically distinct areas have been chosen by the administrators of the reserve for management in accordance with purposes a) or b). The remainder of the reserve they have designated c). For the purposes of this study, three additional areas from this remainder have been delineated and measured. Below are given the mnemonic, the management designation, and the name of each of these twelve areas.

Sas	a	Sassetello
Tro	a	Troscia del porcino
Acq	a	Acquachiara
Sub	b	Subissone
Mar	b	Marzapalo
Vit	b	Vitabbiete
Mac	b	Macchia bruciata
Sam	b	Sambucheto
Tig	b	Tigna
Nor	c	Zona Nord
SuE	c	Zona Sud Est
SuO	c	Zona Sud Ovest

The forestry assessment service of the Riserva Naturale de Monte Rufeno recognizes eleven vegetation types, briefly described as follows:

CER	Woodland dominated by cerro, *Quercus cerris*
LAT	Woodland of mixed broadleaf trees
SCL	Mediterranean sclerophyllous scrub (macchia)
ARB	Various bushes
RIP	River side vegetation
CAS	Woodland dominated by chestnut, *Castanea sativa*
CPU	Woodland dominated by both cerro, *Quercus cerris* and roverella, *Quercus pubescens*
ROV	Woodland dominated by roverella, *Quercus pubescens*
RUP	Wooded cliff
PAS	Abandoned pasture in early succession with bushes and trees
CON	Native and exotic conifers planted thirty years ago on abandoned farmland, including *Pinus pinaster, P. nigra, P. pinea, P. strobus, P. halepensis, P. radiata*, and *Cupressus arizonica*.

TABLE 1. Amounts in hectares of the vegetation types (labelling the rows) present in the management areas (labelling the columns) of the Riserva Naturale di Rufeno, Lazio, Italy.

	Sas	Tro	Acq	Sub	Mar	Vit	Mac	Sam	Tig	Nor	SuE	SuO
CER	65	80	53	52	79	49	75	87	197	114	126	128
LAT	11	58	0	6	13	31	31	10	59	0	38	47
SCL	20	16	0	0	102	0	0	0	0	0	0	0
ARB	0	0	0	2	1	23	6	10	2	0	2	8
RIP	0	0	0	2	0	0	0	0	0	0	0	1
CAS	0	0	0	0	0	0	0	12	0	0	0	0
CPU	0	0	0	0	0	0	0	2	0	0	1	0
ROV	0	0	0	0	0	0	0	5	0	0	5	0
RUP	0	0	0	0	0	0	0	3	0	0	0	0
PAS	0	0	0	0	0	0	0	5	2	0	0	3
CON	5	0	0	15	24	13	7	97	16	31	86	70

For each of the twelve management areas, the forestry assessment service has determined the number of hectares of each vegetation type that occurs there. These data are presented in table 1.

ASSESSMENT OF THE MANAGEMENT AREAS

Measures of diversity, contribution to diversity, and efficiency were calculated for each management area in the Riserva Naturale di Monte Rufeno using the data presented in table 1. Here the entities being conserved are the vegetation types, and the unit of amount is hectares. These calculated measures are presented in table 2.

The total amount of vegetation preserved is 2006 hectares with eleven vegetation types represented at a diversity of 2.74. The most diverse area is Vit with four types represented nearly equally and a diversity of 3.31. The next most diverse area, Sam, had nine of the eleven types very unevenly represented and a diversity of 3.07. Two other areas, Mar and SuO, have diversity slightly higher than the diversity of the whole reserve. The remaining eight have lower diversities. Acq is the least diverse, with only one vegetation type.

If the reserve were homogeneous, i.e., each area had vegetation types in the same proportions as those of the whole reserve, then the contribution to diversity of any area would be zero. Of the twelve areas, six have positive and six have negative contributions to the diversity of the whole reserve. The highest contribution is made by Mar, one of the larger areas, with five types and a diversity about the same as that of the reserve. It is the major conserver of mediterranean scrub. The next to highest contributor to diversity is Sam, a large, diverse area and the only conserver of chestnut woodland or wooded cliff. Tig has the largest negative contribution to reserve diversity; it is a large area conserving (redundantly in this sense) vegetation types already well represented in the other areas. The large negative contribution of Nor indicates similar redundancy.

TABLE 2. Diversity measure for the Riserva Naturale de Monte Rufeno and its twelve management areas. Columns are labelled as follows: Amo: amount; Ric: richness; Div: diversity; CD: contribution to diversity; DA: diversity-amount; CDA: contribution to diversity amount; and Eff: efficiency.

	Amo	Ric	Div	CD	DA	CDA	Eff
Riserva	2006	11	2.74	2.74	5498	5498	2.74
Sas	101	4	2.14	-0.02	216	235	2.32
Tro	154	3	2.37	0.02	365	464	3.01
Acq	53	1	1.00	-0.08	53	-004	-0.08
Sub	77	5	1.99	-0.03	154	147	1.91
Mar	219	5	2.76	0.20	604	960	4.38
Vit	116	4	3.31	0.06	384	434	3.74
Mac	119	4	2.12	-0.03	253	267	2.25
Sam	231	9	3.07	0.15	709	895	3.88
Tig	276	5	1.79	-0.17	494	460	1.67
Nor	145	2	1.51	-0.13	218	161	1.11
SuE	258	6	2.69	0.03	694	765	2.97
SuO	257	6	2.80	0.03	720	757	2.95

An area's contribution to its reserve's diversity-area is almost always positive, because of contributing more amount to the conservation objective, even if it is somewhat redundant. In the imaginary homogeneous reserve described earlier, where contribution of each area to diversity would be zero, the contribution of each area to diversity-amount would equal its own diversity-amount, and its efficiency would equal its own diversity. Three areas, Acq, Tig, and Nor, had contributions to the reserve's diversity-amount that was as much as tens of type hectares below their own diversity amount. The unusual negative contribution of Acq is a consequence of its small size and redundant conservation of the most common vegetation type. Two areas, Sas and Mac, had slightly negative contributions to diversity but contributions to diversity-amount in excess of their own.

The most efficient area is Mar with a diversity amount contribution 356 type hectares above its own diversity-amount, followed in order by Sam (186 type hectares above), Vit (50), Tro (99), SuE (77), and SuO (36). If efficient conservation of diversity-amount were the only consideration in setting management policy, the management designation of some of the areas in Riserva Naturale di Monte Rufeno could be questioned. Mar and Sam are the two areas that contribute by far most efficiently and effectively to conserving diversity-amount in the nature reserve. These two areas contain most of the mediterranean scrub and all of the chestnut woodland. Native mediterranean scrub may have been more widespread but more recently destroyed by development, disease, and harvesting. This possibility is currently under study at the University of Viterbo. The origin of chestnut in Italy is still an open question: is it native or was it originally introduced by humans? The chestnut woodland in this reserve was planted over a hundred years ago and later abandoned. These two areas have not been designated for strict conser-

vation. Among the six most efficient of the twelve areas, only Tro has been designated for strict conservation, whereas Acq, the smallest and least efficient of the twelve areas, is among the three so designated.

Contribution to the amount of biological diversity conserved is one of several potentially compelling considerations that could influence natural area management decisions. In the example here, the three areas designated for strict conservation are the three areas least "contaminated" by the presence of unnatural conifer plantations. Should the presence of an unnatural feature (an old logging road, an abandoned cabin, trees planted by people, etc.) disqualify an otherwise diverse, natural area from protection? Acq is a 53 hectare stand of *Quercus cerris*. Although this is the most common vegetation type, comprising over half of the vegetation conserved in the reserve, this stand may be especially pristine, have an especially rich or original understory, or be particularly amenable to effective protection. Other possibly compelling reasons why an area should deserve stricter protection include its role as a faunal habitat, as a watershed, or as a component of a landscape viewed from afar. The managers of the Riserva Naturale di Monte Rufeno have undoubtedly considered such factors in choosing areas for strict conservation.

The inclusion of human economic activity as a management objective for a natural area can be very important also. Economic pressures to use or develop natural areas are often very strong. Political support for any conservation at all may become possible only if compatible economic activity is allowed. In some cases, it is important to conserve examples of human economic activity that form a part of a naturally balanced ecosystem. Examples of traditional agricultural technology, whose wisdom may be vitally important to our future economy, can be preserved in this way.

Two of the three areas designated for recreational use are from among the six areas that most efficiently represent diversity-amount. Recreational use can impact unfavorably on conservation objectives; however, there may be compelling reasons for these choices. One important reason for conserving nature is to let people experience it. Designating some of the diverse representative areas for people to enjoy enables them to realize this important conservation objective. Furthermore, the personal experience of diverse natural areas may increase people's awareness of their value and broaden future political support for their establishment and protection.

Efficient and effective contribution to the amount of diversity conserved in a nature reserve is an important quality of the areas of a reserve that should enjoy stricter protection, or of areas that should be brought under protection in the future. The objective, quantitative measures of diversity contribution that we present here may be useful considerations, among others, with which to guide management decisions.

ACKNOWLEDGMENTS

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NEW AND RECONSIDERED MEXICAN ACANTHACEAE. V.

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As study of the approximately 360 species of Mexican Acanthaceae progresses, numerous undescribed species have become evident. Five of these, *Chileranthemum lottiae*, *Justicia torresii*, *J. valvata*, *Pseuderanthemum floribundum*, and *Ruellia guerrerensis*, are described below. Also, several poorly known and reconsidered species are discussed.

NEW SPECIES

Chileranthemum lottiae T. F. Daniel, sp. nov.—TYPE: MEXICO. Guerrero: Acapulco, 23 Dec 1958, *Paray 2857* (holotype: ENCB!; isotypes: MEXU! MICH!). Fig. 1.

Frutex usque ad 2 m altus. Folia subsessilia vel petiolata, laminae ovato-ellipticae vel ellipticae vel lanceolato-ellipticae, 2.7–19.5 cm longae, 1.1–7.2 cm latae, 2–4.8plo longiores quam latiores. Thyrsi densiflori usque ad 15.0 cm longi et 1.4–2.2 cm diametro in medio. Bracteae caducae, lanceolato-subulatae, 4–8 (–12) mm longae, 0.5–1 mm latae. Bracteolae 2–7 mm longae, 0.4–0.7 mm latae. Calyx 5.5–13 mm longus lobis linearibus vel lanceolato-subulatis, 5–11 mm longis, basi 0.5–0.8 mm latis. Corolla purpurea, 13–21 mm longa. Stamina inclusa, 3 mm longa et stylus exsertus, 10–12 mm longus vel stamina exserta, 6–10 mm longa et stylus inclusus, 3.5–5.8 mm longus. Capsula 19–27 mm longa, puberula.

Shrub to 2 m tall; young stems terete to quadrate, evenly pubescent with antrorse to flexuose to retrorse, eglandular trichomes 0.1–0.5 mm long, the trichomes often becoming concentrated in 2 lines on mature stems, older stems blistered (especially along corners of quadrate internodes), becoming glabrate as epidermis exfoliates. Leaves subsessile to petiolate; naked portion of petioles to 10 mm long; blades ovate-elliptic to elliptic to lance-elliptic, 2.7–19.5 cm long, 1.1–7.2 cm wide, 2–4.8 times longer than wide, acute to acuminate (to subfalcate) at apex, attenuate (often decurrent along petiole nearly to or to node) at base, surfaces sparsely pubescent when young, later glabrous or nearly so, margin entire to subsinuate. Inflorescence a narrow (1.4–2.2 cm in diameter near midpoint, exclusive of corollas and capsules), densely flowered thyrse to 15.0 cm long, thyrse axis pubescent with flexuose, usually somewhat appressed, eglandular trichomes to 0.5 mm long; dichasia sessile or borne on peduncles to 3 mm long, many-flowered, often congested so as to obscure thyrse axis; flowers borne on pedicels 1–5 mm long. Bracts caducous, lance-subulate, 4–8 (–12) mm long, 0.5–1 mm wide, pubescent with flexuose to antrorse-appressed trichomes 0.1–0.3 mm long. Bractlets and secondary bractlets subulate, 2–7 mm long, 0.4–0.7 mm wide, pubescent like bracts. Calyx 5.5–13 mm long during anthesis, often somewhat accrescent in fruit, tube 0.5–1 mm long, lobes linear to lance-subulate, 5–11 mm long, 7–13

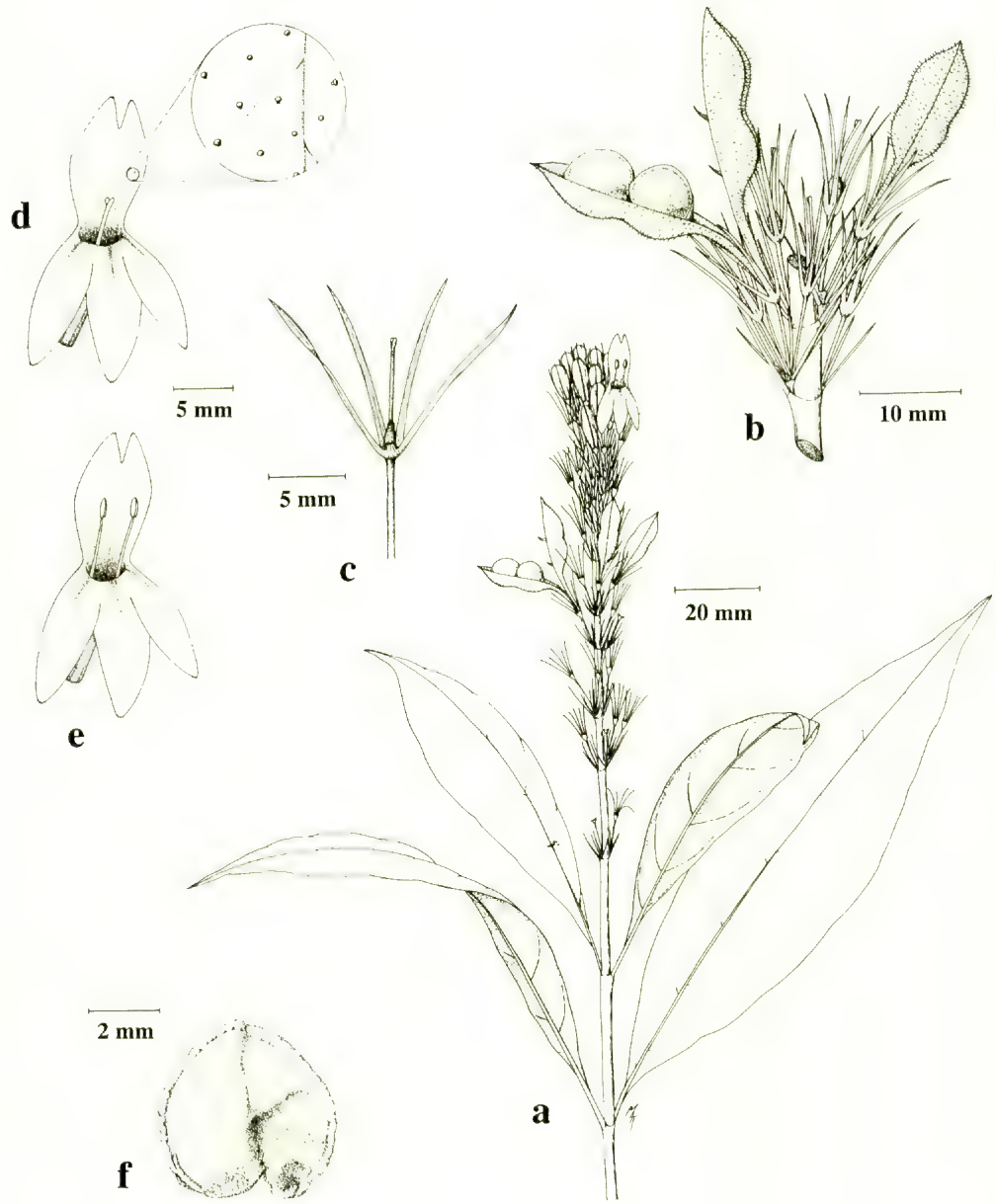

FIG. 1. *Chileranthemum lottiae*. a. Habit (*Paray 2858*). b. Portion of inflorescence with capsules (*Paray 2857*). c. Calyx (with one lobe removed) and gynoecium (*Paray 2858*). d. Long-styled (pin) flower with enlargement showing pubescence (*Paray 2857*). e. Short-styled (thrum) flower (*Paray 2858*). f. Seed (*Paray 2857*). Drawn by Mary Ann Tenorio.

times longer than tube, 0.5–0.8 mm wide at base, abaxial surface sparsely pubescent with mostly antrorse, eglandular trichomes 0.05–0.2 mm long, and often with short-stipitate glands up to 0.05 mm long (glandular-puberulent), adaxial surface glandular-puberulent, the calyx rarely with 2 lobes united for most of their length. Corolla blue-purple with a white stripe on lower lip, 13–21 mm long, externally glabrous, inner surface glandular-puberulent, common portion of lower lip and distal portion of tube bearded with eglandular trichomes to 0.2 mm long, margins

of lobes ciliolate with eglandular trichomes to 0.1 mm long, tube 6.5–11 mm long, upper lip 6.5–9.5 mm long with lobes 1.5–2.5 mm long, lower lip 7.5–11 mm long with elliptic to obovate-elliptic lobes 6–10 mm long, 2.5–4.5 mm wide. Stamens of "pin flowers" included, 3 mm long, thecae 1.6 mm long, stamens of "thrum flowers" exserted, 6–10 mm long, thecae 1.5–2.3 mm long; pollen (Fig. 2a–c) prolate, 3-colporate, 6-pseudocolpate, the 2 pseudocolpi in each mesocolpium often fused into a pseudocolpal ellipse, surface reticulate; staminodes 0.2–0.5 mm long. Style curved to recurved just proximal to stigma, glabrous or sparsely pubescent with eglandular trichomes (sometimes restricted to distal portion), style of "pin flowers" exserted, 10–12 mm long, style of "thrum flowers" included, 3.5–5.8 mm long; stigma subfunnelform to bilobed with lobes 0.1–0.2 mm long. Capsule 19–27 mm long, pubescent with straight or bent, eglandular trichomes 0.05–0.4 mm long, stipe 8–13 mm long, head 11–16 mm long. Seeds subcircular in outline, 5–5.5 mm in diameter, surfaces smooth, glabrous.

Phenology. Flowering: August and December; fruiting: December.

Distribution (Fig. 3). West-central Mexico (Guerrero and Jalisco); rocky hills near the coast in regions of tropical deciduous forest; 50–100 m.

PARATYPES. **Mexico.** Guerrero: Acapulco, 23 Dec 1958, *Paray 2858* (ENCB).—JALISCO: Mpio. La Huerta, Rancho Cuixmala, Cumbres 1, Arroyo Cajones, ca. 3 km inland from Puerto Vallarta-Barra de Navidad hwy, 19 Aug 1991, *Lott et al. 3794* (CAS, MEXU, MICH, NY, UCR, US); near Playa Cuastecomate, 8 km NW of Navidad, 11–12 Dec 1959, *McVaugh & Koelz 1686* (MICH).

Like the two previously described species of *Chileranthemum* Oerst., *C. lottiae* is heterostylous. For example, the holotype and isotypes possess long-styled or "pin" flowers, whereas the paratype from the same locality has short-styled or "thrum" flowers. Heterostyly has also been reported in three other genera of tribe Justicieae subtribe Odontoneminae, *Odontonema* Nees, *Oplonia* Raf., and *Pseuderanthemum* Radlk. These genera and *Chileranthemum* appear to form a distinct lineage within the subtribe (Daniel & Chuang, unpubl.).

The three species of *Chileranthemum* are geographically separated from one another. Morphologically, characters of the calyx have been used to distinguish *C. violaceum* Miranda from *C. trifidum* Oerst. *Chileranthemum lottiae* more closely resembles the latter species in features of the calyx and can be distinguished from both *C. violaceum* and *C. trifidum* by its pubescent capsules. The following key distinguishes the species of this Mexican genus.

1. Calyx tube (2–) 3–6 mm long, calyx lobes ovate to broadly triangular, 3–7 mm long, 2–3.5 mm wide at base; southern Mexico (Oaxaca and Chiapas). *C. violaceum.*
1. Calyx tube 0.5–1.5 mm long, calyx lobes linear to lance-subulate to subulate, 4–11 mm long, 0.5–1 mm wide at base.
   2. Inflorescence of axillary or terminal, few-flowered, open cymes to 3 cm long; capsule 12–18 mm long, glabrous; northeastern Mexico (Hidalgo, Puebla, Veracruz). *C. trifidum.*
   2. Inflorescence of terminal, many-flowered, narrow thyrses to 15 cm long; capsule 19–27 mm long, pubescent; west-central Mexico (Guerrero and Jalisco). *C. lottiae.*

Chileranthemum lottiae is named in honor of Emily Lott who collected a paratype of it and whose many excellent collections of Acanthaceae from coastal Jalisco have greatly enhanced our knowledge of the family.

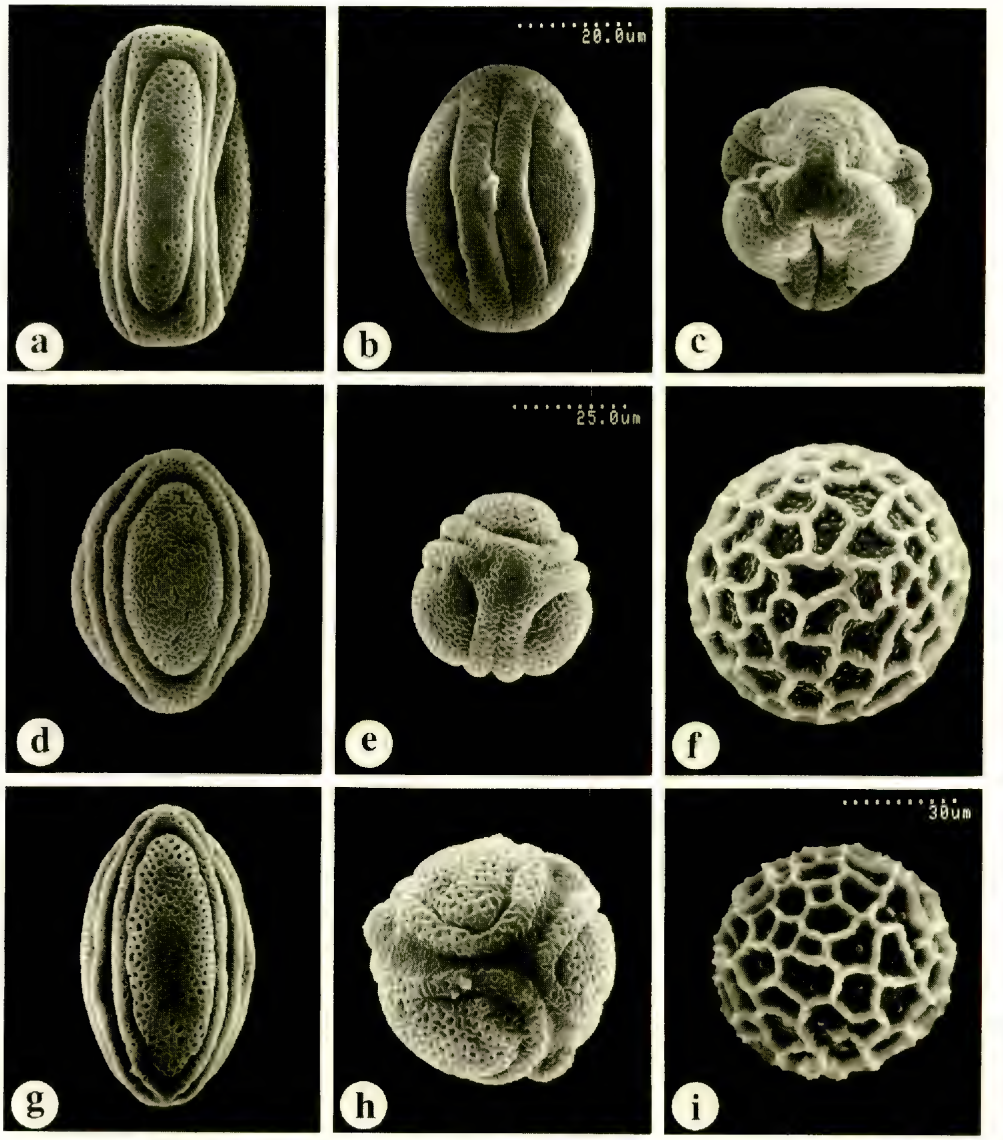

FIG. 2. Scanning electron micrographs of pollen. a. *Chileranthemum lottiae* (*Paray 2858*), intercolpal view. b. *C. lottiae* (*Paray 2858*), colpal view. c. *C. lottiae* (*Paray 2858*), polar view. d. *Pseuderanthemum floribundum* (*Daniel 5381*), intercolpal view. e. *Pseuderanthemum floribundum* (*Daniel 5381*), polar view. f. *Ruellia guerrerensis* (*Hinton et al. 11296*). g. *Pseuderanthemum pihuamoense* (*Daniel et al. 6283*), intercolpal view. h. *P. pihuamoense* (*Daniel et al. 6283*), polar view. i. *Ruellia rosea* (*Daniel & Baker 3736*).

Pseuderanthemum floribundum T. F. Daniel, sp. nov.—TYPE: MEXICO. Oaxaca: along Mex. 131 between Puerto Escondido and Sola de Vega, 26.9 km N of San Gabriel Mixtepec, 1275 m, 14 Nov 1987, *Daniel 5381* (holotype: CAS!; isotypes: C! DUKE! ENCB! F! GH! K! MEXU! MICH! MO! NY! US!). Fig. 4.

Herba perennis usque ad 1.5 m alta caulibus crassis. Laminae foliorum late ellipticae vel late ovato-ellipticae, 10–28 cm longae, 5.5–21.5 cm latae, 1.3–1.8plo longiores quam latiores. Inflorescentia paniculata composita multiflora usque ad 35 cm longa ramis glandulosis. Bracteae inflorescentiae subfoliaceae sessiles

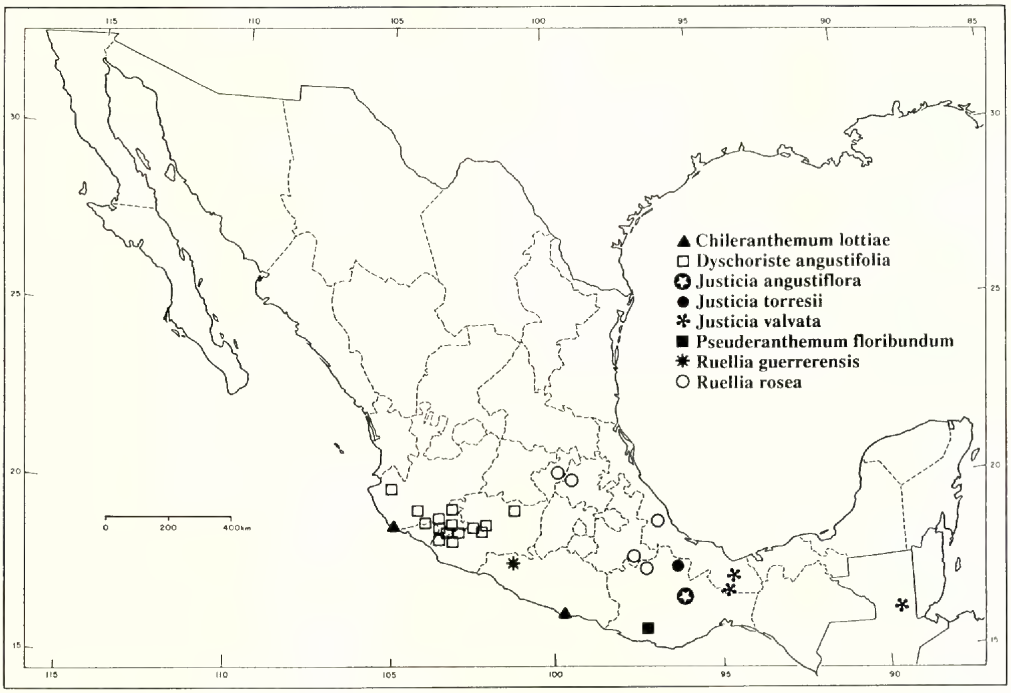

FIG. 3. Distribution of *Chileranthemum lottiae*, *Dyschoriste angustifolia*, *Justicia angustiflora*, *J. torresii*, *J. valvata*, *Pseuderanthemum floribundum*, *Ruellia guerrerensis*, and *R. rosea*.

amplectentes. Bracteae florales anguste ellipticae vel ovatae, 2–6 mm longae, 0.8–1.8 mm latae. Calyx 4–7 mm longus, extus glandulosus. Corolla roseo-purpurea, bilabiata, 29–35 mm longa. Capsula 21–25 mm longa, glandulosa. Semina 4, subcordata, 4–5 mm longa, 3.7–4 mm lata.

Perennial herb to 1.5 m tall, sometimes rooting at nodes; young stems quadrate-sulcate, up to 13 mm across one side, pubescent with flexuose to flexuose-antrorse, eglandular trichomes 0.3–1 mm long, the trichomes disposed throughout internode although concentrated in 2 lines, pith of mature stems large and styrofoamlike. Leaves present during anthesis, sessile (distally) to petiolate (proximally); petioles purplish when fresh, up to 15.5 cm long, shorter than blade, winged from blade, wing up to 2.8 cm wide near blade and tapering nearly to or to node; blades somewhat corrugated when fresh, broadly elliptic to broadly ovate-elliptic, 10.0–28.0 cm long, 5.5–21.5 cm wide, 1.3–1.8 times longer than wide, acute at apex, rounded to attenuate at base, adaxial surface sparsely pubescent with cauline type trichomes, abaxial surface pubescent with cauline type trichomes on major veins and with submarginal white sublinear to substellate thickened regions 0.5–1.5 mm long at some vein junctions, margin entire, flat to subrevolute. Inflorescence of axillary (from axils of subfoliose inflorescence bracts) and terminal, pedunculate spicate axes or panicles of spicate axes up to 20 cm long, forming a terminal, subfoliose panicle up to 35 cm long, main inflorescence axis pubescent with an understory of glandular trichomes 0.05–0.2 mm long (glandular-puberulent) and an overstory of flexuose, eglandular trichomes 0.2–0.6 mm long, peduncles up to 80 mm long, pubescent like main inflorescence axis, individual spicate axes glandular-puberulent, subtended by progressively reduced inflorescence bracts; inflorescence bracts sessile-clasping, oblate to circular to broadly ovate-elliptic, 1–19 cm long, 0.8–14 cm wide, 0.8–1.5 times longer than wide, cordate to rounded at

base, emarginate to rounded to acute at apex, proximal inflorescence bracts pubescent like leaves, distal inflorescence bracts usually pubescent like inflorescence axes; flowers arranged in dichasia in axil of a bract, the dichasia sessile, rarely reduced to a single flower, the flowers borne on pedicels to 5 mm long, pedicels glandular-puberulent. Bracts narrowly elliptic to ovate, 2–6 mm long, 0.8–1.8 mm wide, abaxial surface pubescent like rachis or nearly glabrous, margin ciliate with eglandular trichomes up to 0.5 mm long. Bractlets narrowly elliptic to ovate, 2.2–4 mm long, 0.8–1.2 mm wide, pubescent like bracts. Calyx 4–7 mm long, tube 0.5–2 mm long, lobes lance-subulate, 3–5.5 mm long, subequal (up to 1.3 mm different in length), often accrescent in fruit, 2.5–7 times longer than tube, abaxial surface and margin glandular-puberulent. Corolla pink-purple (drying dark purple) with a solid white area on proximal portion of lower-central lobe, 29–35 mm long, external surface of tube glabrous, that of throat and limb very sparsely pubescent with scattered, mostly eglandular trichomes 0.1–0.3 mm long, margins of lobes sparsely ciliate with similar trichomes, tube cylindric, 18–21 mm long, 1.4–2 mm in diameter (same at base and apex), throat 1.5–3 mm long, 2–3.5 mm in diameter, limb 18–24 mm in diameter, upper lip 8–11 mm long with lobes reflexed, elliptic to obovate-elliptic, 8–11 mm long, 4.7–8.5 mm wide, lower lip 9–14 mm long with lateral lobes elliptic to obovate-elliptic, 6–9.7 mm long, 5–7.5 mm wide, lower-central lobe broadly elliptic to subcircular, 7.5–11 mm long, 5–7.8 mm wide. Stamens 3.5 mm long, exserted 1–1.7 mm beyond mouth, inserted 1.5–2 mm below mouth, filaments 0.8–1 mm long, sparsely pubescent with eglandular and inconspicuous glandular trichomes, thecae parallel, equally inserted, subequal in length, 2.4–2.8 mm long, sparsely pubescent with eglandular trichomes; pollen (Fig. 2d, e) prolate, 3-colporate, 6-pseudocolpate, the 2 pseudocolpi in each mesocolpium fused into a pseudocolpal ellipse, surface reticulate; staminodes 0.5 mm long. Style pink-purple, 21–23 mm long, exserted 0.5–3 mm beyond anthers, pubescent with straight to flexuose, ascendant, eglandular trichomes 0.05–0.2 mm long, distal portion glabrous; stigma lobes 0.1 mm long. Capsule 21–25 mm long, sparsely glandular-puberulent, stipe 8–11 mm long, head 13–15 mm long, retinacula 2.2–3 mm long, the pair 3–4 mm distant in a valve. Seeds 4, subcordate, plano-convex, 4–5 mm long, 3.7–4 mm wide, 1.1–1.3 mm thick, both surfaces verrucose and with irregular anastomozing ridges.

Phenology. Flowering and fruiting: November.

Distribution (Fig. 3). Known only from the Pacific slopes of the Sierra Madre Sur in southern Oaxaca; moist broadleaf evergreen forest with pines; ca. 1275 m.

PARATYPES. **Mexico.** OAXACA: seeds of type (*Daniel 5381*) grown at San Francisco Conservatory of Flowers in 1988–1991, (CAS, K, MEXU, RSA, TEX). State and locality undetermined: seed no. 552 of E. Alexander and J. McDougal grown at Royal Botanic Gardens at Kew in 1947 (K).

Seeds of *Pseuderanthemum floribundum* were collected by E. J. Alexander and J. G. McDougal in Mexico prior to November 1947 and subsequently grown at the Royal Botanical Gardens at Kew. Specimens of the resulting cultivated plants, which flowered in November, 1947, are extant at K. I have not seen any field-collected specimens of this species made by Alexander and McDougal.

This is the largest and showiest species of *Pseuderanthemum* in Mexico. It can be distinguished from all other North and Central American species by its 1) thick and somewhat fleshy stems; 2) large and somewhat corrugated leaf blades; 3) large, open, and pyramidal panicles; and 4) distinctive floral form. Corollas of *P. floribundum* are subhorizontally oriented and have a distinctly bilabiate limb.

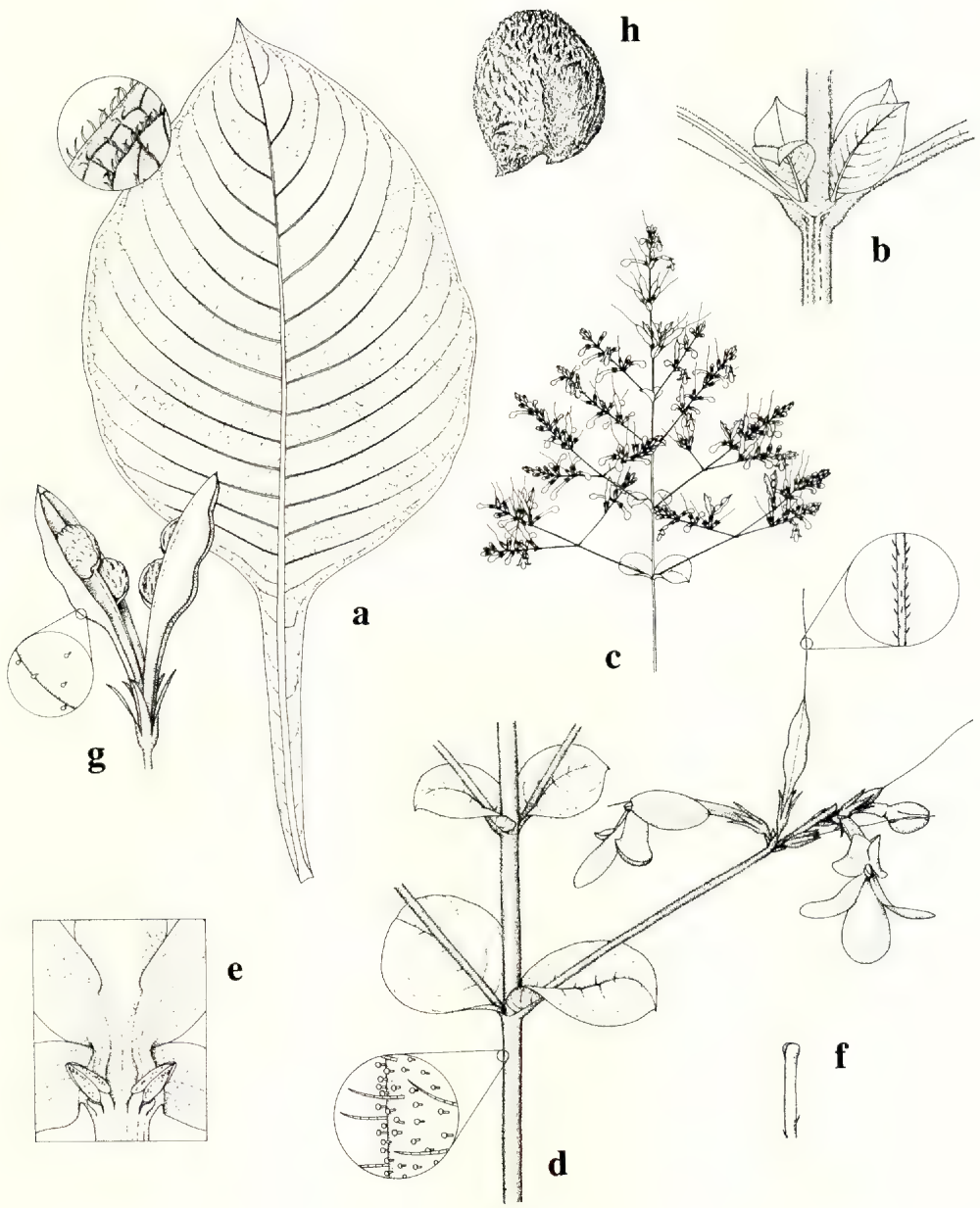

FIG. 4. *Pseuderanthemum floribundum* (*Daniel 5381*). a. Leaf from near base of plant with enlargement showing pubescence and submarginal thickened regions, ×0.33. b. Vegetative node, ×0.5. c. Inflorescence, ×0.16. d. Portion of inflorescence with flowers and fruit and with enlargements showing pubescence of rachis and style, ×1. e. Cut-open view of corolla showing androecium, ×3. f. Distal portion of style and stigma, ×13. g. Opened capsule with enlargement showing pubescence, ×1.8. h. Seed, ×4.5. Drawn by Mary Ann Tenorio.

Other North and Central American species of the genus generally have subvertically oriented flowers with a subrotate limb. In these floral characters, *P. floribundum* resembles most species of *Odontonema*. This resemblance possibly represents floral convergence for a similar pollinator (e.g., hummingbirds, although floral visitors to *P. floribundum* are not known). Flowers of *Pseuderanthemum* (including *P. floribundum*) differ from those of *Odontonema* by their bicolored corollas with reflexed upper lips. In general form, the flowers also resemble those

of *Chileranthemum*. Flowers of the latter genus have considerably shorter corolla tubes, however. The systematic relationships among these three genera deserve considerable further attention.

Ruellia guerrerensis T. F. Daniel, sp. nov.—TYPE: MEXICO. Guerrero: Distr. Mina, Manchon [El Manchón], 3 Dec 1937, *Hinton et al. 11296* (holotype: K!; isotypes: LL! MICH! RSA! UC! US!). Fig. 5.

Frutex usque ad 1 m altus. Caules juniores quadrati vel quadrato-sulcati, internodis plus minusve uniformiter pubescentibus trichomatibus flexuosis vel retrorsis eglandulosis 0.1–0.8 mm longis. Folia petiolata, laminae ovatae vel ovato-ellipticae, 4.0–13.5 cm longae, 1.5–6.8 cm latae, 2–2.7plo longiores quam latiores. Inflorescentia thyrsiformis thyrso terminali multifloro glanduloso. Bracteae petiolatae glandulosae, inferiores foliaceae, superiores anguste ellipticae vel lineares. Bracteolae lineares, 33–60 mm longae, 0.6–1.2 mm latae. Calyx 20–37 mm longus, glandulosus. Corolla lutea, 60–77 mm longa, extus glandulosa, fauce 12–15 mm longa, 8–9.5 mm diametro in medio, limbo 24–29 mm diametro. Stamina 19–28 mm longa thecis 5.5–6.6 mm longis. Capsula glabra.

Shrub to 1 m tall; younger stems quadrate to quadrate-sulcate, internodes more or less evenly, often sparsely, pubescent with flexuose to retrorse, eglandular trichomes 0.1–0.8 mm long, nodes often with clusters of somewhat longer eglandular trichomes. Leaves petiolate; petioles to 2.5 cm long (naked portion to 1.3 cm long); blades ovate to ovate-elliptic, 4.0–13.5 cm long, 1.5–6.8 cm wide, 2–2.7 times longer than wide, acuminate at apex, attenuate to long-attenuate (often tapering to node) at base, surfaces pubescent with flexuose, eglandular trichomes to 1.2 mm long, margin entire to somewhat sinuate-denticulate. Inflorescence a terminal, leafy (near base) thyrse, rachis pubescent with straight to subflexuose, glandular and eglandular trichomes to 1 mm long; dichasia pedunculate, many-flowered, peduncles (arising from axils of distal several pairs of leaves at base of thyrse and from bracts near apex of thyrse) to 6.5 cm long, pubescent like rachis; flowers borne on pedicels 2–12 mm long, pedicels pubescent like rachis. Bracts foliose at base of thyrse, gradually reduced acropetally, bracts near midthyrse 40-50 mm long, petioles to 25 mm long, blades ovate-elliptic to elliptic, 20–27 mm long, 3.5–7.5 mm wide, distal bracts reduced to 26 mm long and 2.5 mm wide with narrowly elliptic to linear blades, bracts near midthyrse and distal bracts pubescent like rachis. Bractlets and secondary bractlets linear, 33–60 mm long, 0.6–1.2 mm wide, pubescent like rachis. Calyx 20–37 mm long, tube 3–4.5 mm long, lobes subequal, linear-subulate, 17–31 mm long, 4.7–8.3 times longer than tube, 1–2 mm wide, pubescent like rachis. Corolla yellow, 60–77 mm long, externally pubescent with flexuose, glandular trichomes to 0.5 mm long, tube (from base of corolla to point of attachment of stamens) 37–49 mm long, throat 12–15 mm long, neither well differentiated from tube nor saccate, 8–9.5 mm in diameter near midpoint, limb 24–29 mm in diameter with lobes subelliptic, 9–11 mm long, 7.5–10 mm wide. Stamens exserted, 19–28 mm long, thecae 5.5–6.6 mm long; pollen (Fig. 2f) spherical, 3-porate, surface reticulate-homobrochate, lumina filled with low rounded bumps. Style 65–82 mm long, pubescent with eglandular trichomes; stigma lobes unequal, one 1.5–2 mm long, the other 0.5–1.2 mm long. Capsule (possibly immature) clavate, 18–19 mm long, glabrous, stipe 4–7 mm long, head 12–14 mm long. Seeds not seen.

Phenology. Flowering and fruiting: December.

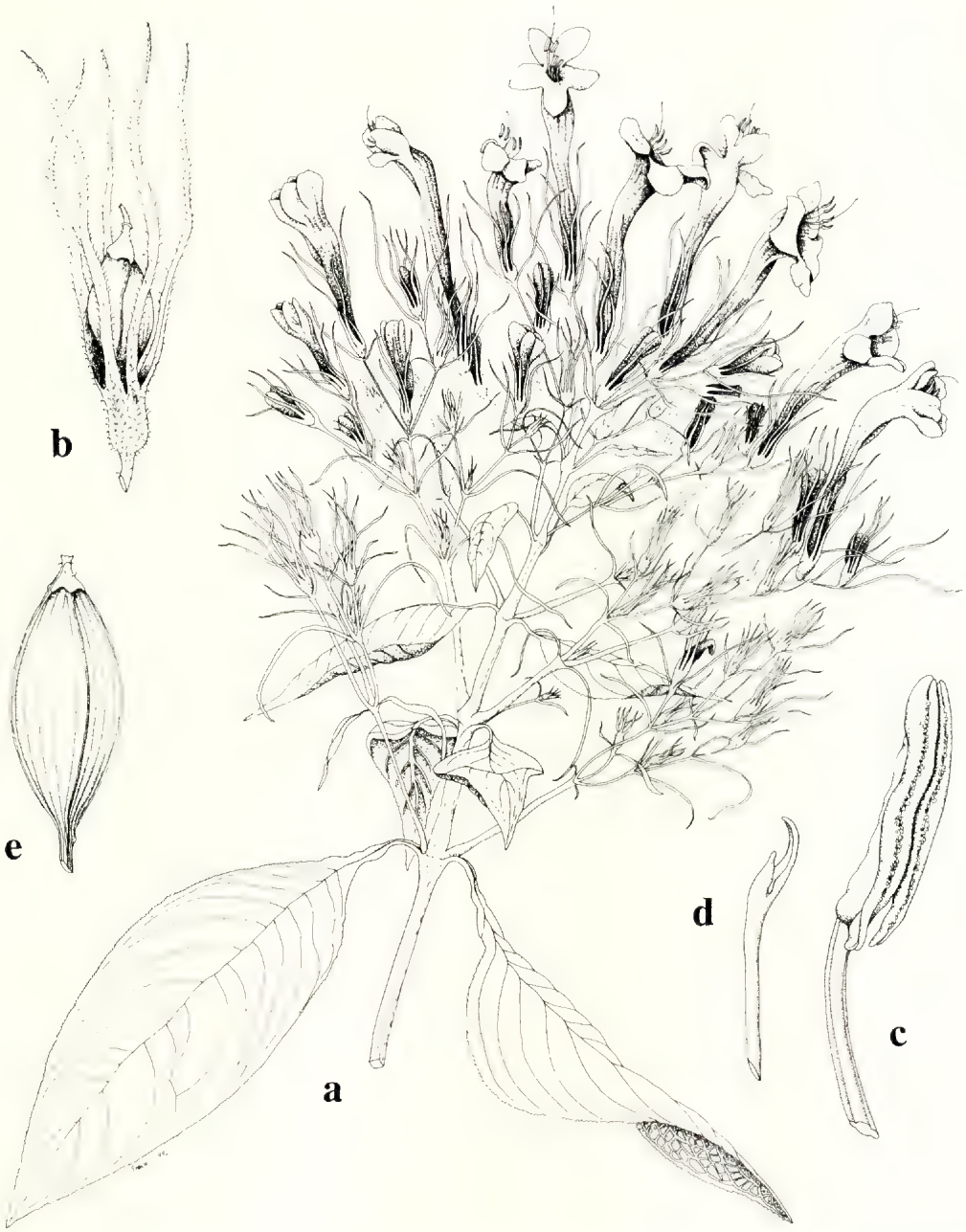

FIG. 5. *Ruellia guerrerensis* (*Hinton et al. 11296*). a. Habit with flowers, ×0.5. b. Calyx and immature capsule, ×1.5. c. Distal portion of stamen, ×6. d. Distal portion of style and stigma, ×4.8. e. Capsule, ×2.1. Drawn by Sheva Myers.

Distribution (Fig. 3). Southwestern Mexico (northwestern Guerrero); in a region dominated by oak woodland; ca. 1300 m.

This species is morphologically similar to *Ruellia jaliscana* Standley and *R. sarukhaniana* Ramamoorthy. All three species occur in montane regions of southwestern Mexico. The slight differences in floral form among them suggest specialization for somewhat different pollinators. Unfortunately, floral visitors to these species remain unreported. The three species can be distinguished from one another by the following key.

1. Corolla throat not well differentiated from tube, 12–15 mm long, 8–9.5 mm in diameter near midpoint, the limb 24–29 mm in diameter; thecae 5.5–6.6 mm long; Guerrero. *R. guerrerensis.*
1. Corolla throat subsaccate to saccate, well differentiated from tube, 17–25 mm long, 12–21 mm in diameter near midpoint, the limb 35–45 mm in diameter; thecae 6–13 mm long; Jalisco and Michoacán.
   2. Leaf blades ovate to ovate-elliptic, 35–180 mm wide, 1.5–2.4 times longer than wide; corolla throat 16–21 mm in diameter near midpoint; thecae 6–9 mm long; Jalisco. *R. jaliscana.*
   2. Leaf blades lanceolate to oblanceolate, 20–38 mm wide, 5.3–6.7 times longer than wide; corolla throat 12–13 mm in diameter near midpoint; thecae 12–13 mm long; Michoacán. *R. sarukhaniana.*

Justicia torresii T. F. Daniel, sp. nov.—TYPE: MEXICO. Oaxaca. Dtto. Tuxtepec, Mpio. Santa María Jacatepec, camino a Cosolapa San Antonio, Ejido de San Felipe Tilpa, 13.3 km SO de La Reforma, 17°51'N, 96°03'W, 20 Feb 1988, *Torres C. & Cortes A. 11472* (holotype: CAS!; isotype: MEXU!). Fig. 6.

Herba perennis usque ad 4.5 dm alta. Folia petiolata, laminae ovatae vel lanceolato-ovatae, 2.5–8.5 cm longae, 1.2–4.3 cm latae, 1.6–3.3plo longiores quam latiores. Spicae in axillis foliorum, usque ad 3.0 cm longae, pedunculatae pedunculis usque ad 20 mm longis, (1–) 2–3 (–5)-florae. Bracteolae anguste lanceolatae vel lanceolato-lineares vel lanceolato-subulatae, 6–17 mm longae, 0.8–1.5 mm latae. Calyx 12–14 mm longus, subaequaliter quadrilobus lobis lanci-subulatis. Corolla lutea, (33–) 37–46 mm longa. Stamina 12–14 mm longa thecis sagittatis subaequaliter insertis, 2.8–3.2 mm longis, basi rotundatis. Capsula 24–28 mm longa, extus glandulosa. Semina 5–6 mm longa, 5–5.5 mm lata, papillosa papillis subconicis usque ad 0.5 mm longis.

Perennial herb to 4.5 dm tall; young stems subquadrate, pubescent with flexuose to antrorse to antrorse-appressed, eglandular trichomes 0.3–0.5 mm long, the trichomes ± evenly disposed or mostly concentrated in 2 lines. Leaves petiolate; petioles to 6 mm long; blades ovate to lance-ovate, 2.5–8.5 cm long, 1.2–4.3 cm wide, 1.6–3.3 times longer than wide, (acute to) acuminate at apex, rounded to acute at base, surfaces pubescent mostly along major veins with cauline type trichomes. Inflorescence of pedunculate, few-flowered spikes to 3.0 cm long (including peduncles and excluding flowers) from leaf axils, solitary or opposite at nodes, peduncles to 20 mm long, pubescent with cauline type trichomes; flowers (1–) 2–3 (–5), sessile to subsessile, congested, solitary at spike nodes, pedicels (if present) to 0.5 mm long. Bracts narrowly lanceolate to lance-linear to lance-subulate, 6–17 mm long, 0.8–1.5 mm wide, abaxial surface pubescent with cauline type trichomes and distally with glands (sometimes sparse) 0.1–0.2 mm long as well. Bractlets lance-subulate to subulate, 5–13 mm long, 0.5–1.5 mm wide, pubescent like bracts although the glands usually more conspicuous. Calyx 4-lobed, 12–14 mm long, lobes lance-subulate, subequal, 9–13 mm long, 1.4–1.6 mm wide, abaxially pubescent like bracts. Corolla yellow, (33–) 37–46 mm long, externally pubescent with flexuose, eglandular trichomes 0.2–0.7 mm long, tube (23–) 26–31 mm long, gradually ampliate distally, internally pubescent with reflexed trichomes (sparsely so distally, densely so near base), upper lip 10–16 mm long, entire at apex, lower lip 10–17 mm long with 3 subelliptic lobes 1.4–4 mm long, 1.5–3 mm wide, rounded at apex. Stamens 12–14 mm long, inserted 2–3 mm proximal to mouth of corolla, filaments glabrous, thecae sagittate, subequally inserted, 2.8–3.2 mm long, lacking

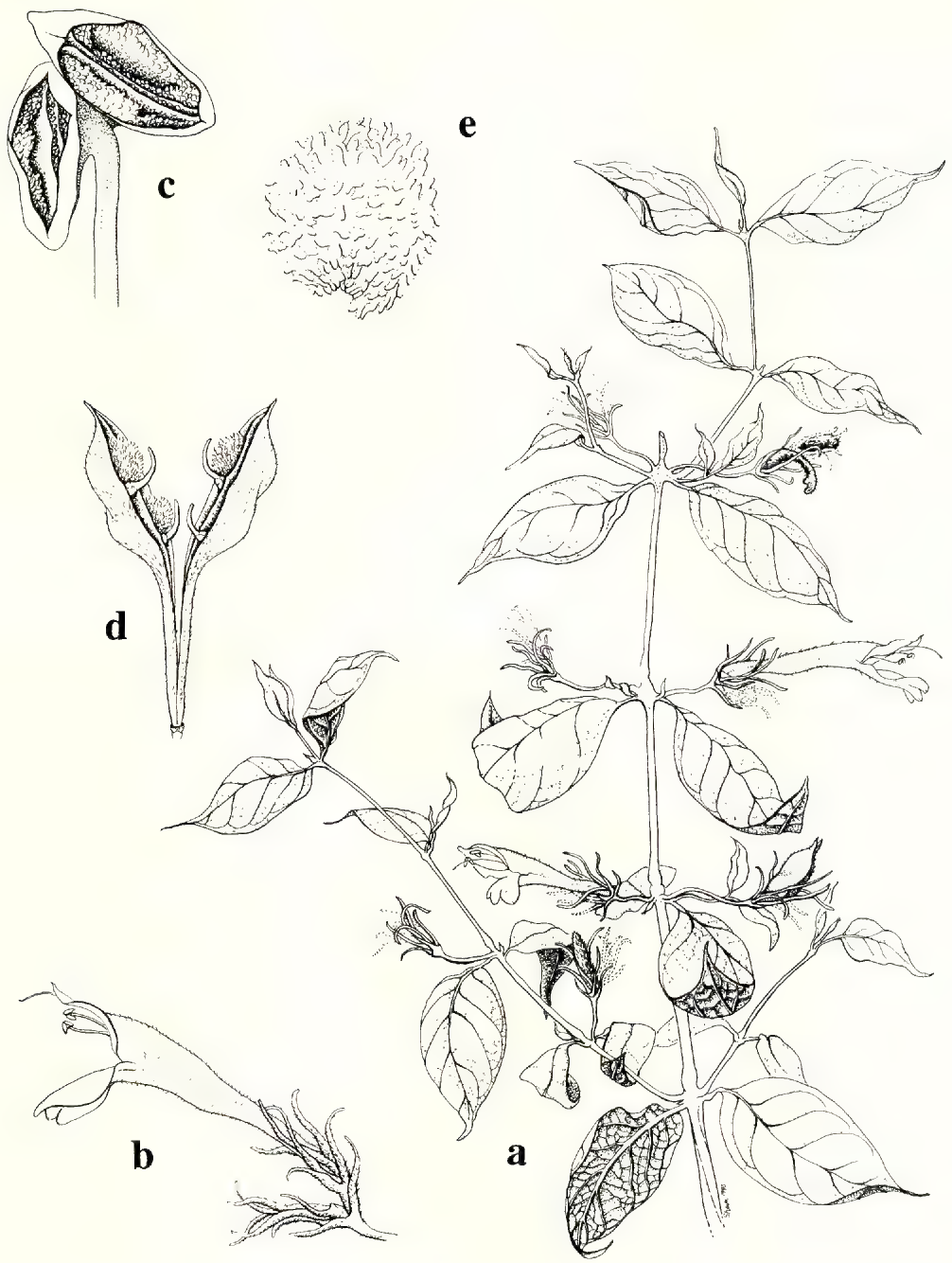

FIG. 6. *Justicia torresii* (*Torres C. & Cortes A. 11472*). a. Habit, ×0.6. b. Dichasium with flower, ×1. c. Distal portion of stamen, ×9. d. Capsule, ×1.5. e. Seed, ×5. Drawn by Sheva Myers.

basal appendages; pollen (Fig. 7d) prolate, 2-colporate with pores in a trema region with 4–6 rows of circular insulae, surface reticulate. Style 35–39 mm long, sparsely pubescent proximally, glabrous distally; stigma subspheric, 0.3–0.4 mm long. Capsule 24–28 mm long, pubescent with straight to retrorse, glandular and eglandular trichomes 0.1–0.3 mm long, stipe 7–11 mm long, head ellipsoid with a slight medial constriction, 16–18 mm long. Seeds 4, green turning brown, flat,

subcircular, 5–6 mm long, 5–5.5 mm wide, surface and margin covered with stout subconic subflexuose papillae to 0.5 mm long, papillae covered with minute spiny projections less than 0.05 mm long.

Phenology. Flowering and fruiting: February.

Distribution (Fig. 3). Known only from northern Oaxaca, Mexico; in lowland rain forest; 300 m.

PARATYPES. **Mexico.** OAXACA: seeds of type (*Torres C. & Cortes A. 11472*) grown at San Francisco Conservatory of Flowers in 1990–1991, *Daniel s.n.* (CAS, DUKE, ENCB, K, MEXU, MICH, MO, NY, RSA, TEX, US).

Justicia torresii is unlike other Mexican and Central American species of the genus and cannot be associated with a subgeneric taxon using the classification of Graham (1988). It has pollen (Graham's "type 7") similar to that found in several sections of the genus (Graham 1988).

Justicia valvata T. F. Daniel, sp. nov.—TYPE: MEXICO. Veracruz: Mpio. Hidalgotitlán, Km 7 camino a la Ecsuadra, 10 Sep 1974, *Dorantes et al. D-3538* (holotype: CAS!). Fig. 8.

Frutex vel arbor parva usque ad 5 m alta. Folia subsessilia vel petiolata, laminae ellipticae, 3.5-24.0 cm longae, 1.4-7.2 cm latae, 2.4-3.3plo longiores quam latiores. Spicae axillares vel terminales, secundae, paniculam formantes floribus sessilibus. Bracteae subfoliaceae, lanceolato-ellipticae vel lanceolato-lineares, 3.5-12 mm longae, 0.7-3 mm latae, caducae. Bracteolae lanceolato-lineares, 2.5-3 mm longae, 0.5-0.6 mm latae. Calyx 9-11.5 mm longus, quinquelobus lobis ovato-triangularibus, valvatis. Corolla flavovirens et purpurascens, 18-25 mm longa, extus glandulosa. Stamina 13 mm longa thecis subaequaliter insertis, 4.5-5 mm longis, basi rotundatis. Capsula ignota.

Shrub to small tree to 5 m tall from aerial roots; young stems quadrate, bifariously pubescent with antrorse, eglandular trichomes 0.2–0.4 mm long, soon glabrate. Leaves subsessile to petiolate; petioles to 15 mm long; blades elliptic, 3.5–24.0 cm long, 1.4–7.2 cm wide, 2.4–3.3 times longer than wide, intergrading with bracts, acuminate to subfalcate at apex, acute to attenuate at base, adaxial surface glabrous, abaxial surface glabrous or with scattered, eglandular trichomes at junctions of major veins. Inflorescence of axillary and terminal pedunculate spikes to 7.5 cm long (including peduncle but excluding flowers), collectively forming a terminal, leafy panicle, peduncles to 35 mm long, rachises pubescent like young stems; flowers sessile, solitary at nodes, borne along only 1 side of rachis. Bracts subfoliose, caducous, lance-elliptic to lance-linear, 3.5–12 mm long, 0.7–3 mm wide, glabrous or sparsely pubescent with antrorse-appressed, eglandular trichomes. Bractlets caducous, lance-linear, 2.5–3 mm long, 0.5–0.6 mm wide, pubescent like bracts. Calyx 5-lobed, 9–11.5 mm long, externally glabrous, lobes valvate-connate, usually each one eventually separating for about 1/2–3/4 the length of the calyx or anterior pair sometimes remaining mostly or completely fused, ovate-triangular, 2.5–3.5 mm wide at base. Corolla greenish yellow with purplish markings, 18–25 mm long, externally pubescent with glandular trichomes 0.2–0.3 mm long, tube 9–14 mm long, upper lip 8–12 mm long, emarginate, lower lip 9 mm long with 3 rounded lobes 1.3–2 mm long, 1.5–2 mm wide. Stamens 13 mm long, thecae subparallel and subequally inserted, 4.5–5 mm long, lacking basal appendages; pollen (Fig. 7e–i) prolate, 4-porate (to 4-subcolporate) with pores in

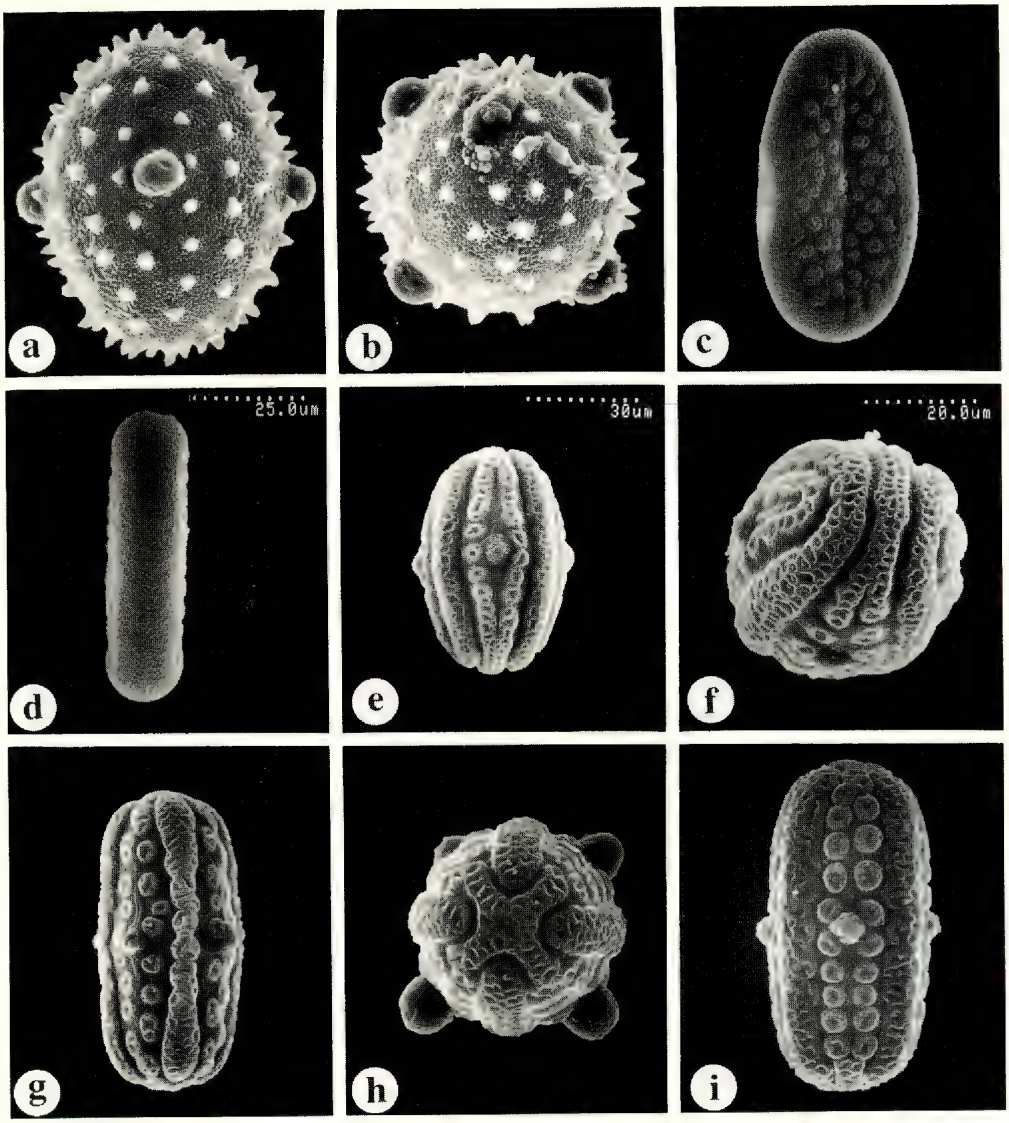

FIG. 7. Scanning electron micrographs of pollen of *Justicia*. a. *J. angustiflora* (*Rivera R. 1255*), colpal view. b. *J. angustiflora* (*Rivera R. 1255*), polar view. c. *J. torresii* (*Torres C. 11472*), colpal view. d. *J. torresii* (*Torres C. 11472*), intercolpal view. e. *J. valvata* (*Dorantes et al. D-3538*), colpal view. f. *J. valvata* (*Dorantes et al. D-3538*), subpolar view. g. *J. valvata* (*Contreras 9311*), intercolpal view. h. *J. valvata* (*Vázquez T. et al. V-2582*), polar view. i. *J. valvata* (*Vázquez T. et al. V-2582*), colpal view.

a trema region containing 2 longitudinal rows of circular insulae, surface reticulate. Style 18–24 mm long, glabrous. Capsule not seen.

Phenology. Flowering: September and November–December.

Distribution (Fig. 3). Southern Mexico (Veracruz) and northern Guatemala (Petén); lowland rain forest ; 100–150 m.

PARATYPES. **Guatemala.** PETÉN: Los Arcos, Cadenas Rd, on Km 143, W, 9 Dec 1969, *Contreras 9311* (LL). **Mexico.** VERACRUZ: Mpio. Hidalgotitlán, Benito Juárez segundo, 17°47'N, 94°39'W, 2 Nov 1978, *Castillo C. 364* (F); Mpio. Hidalgotitlán, 7 km NW del Campamento Hermanos Cedillo por la brecha a La Escuadra, 17°16'N, 94°36'W, 15 Jan 1975, *Vázquez et al. V-1752* (F); Mpio. Jesús

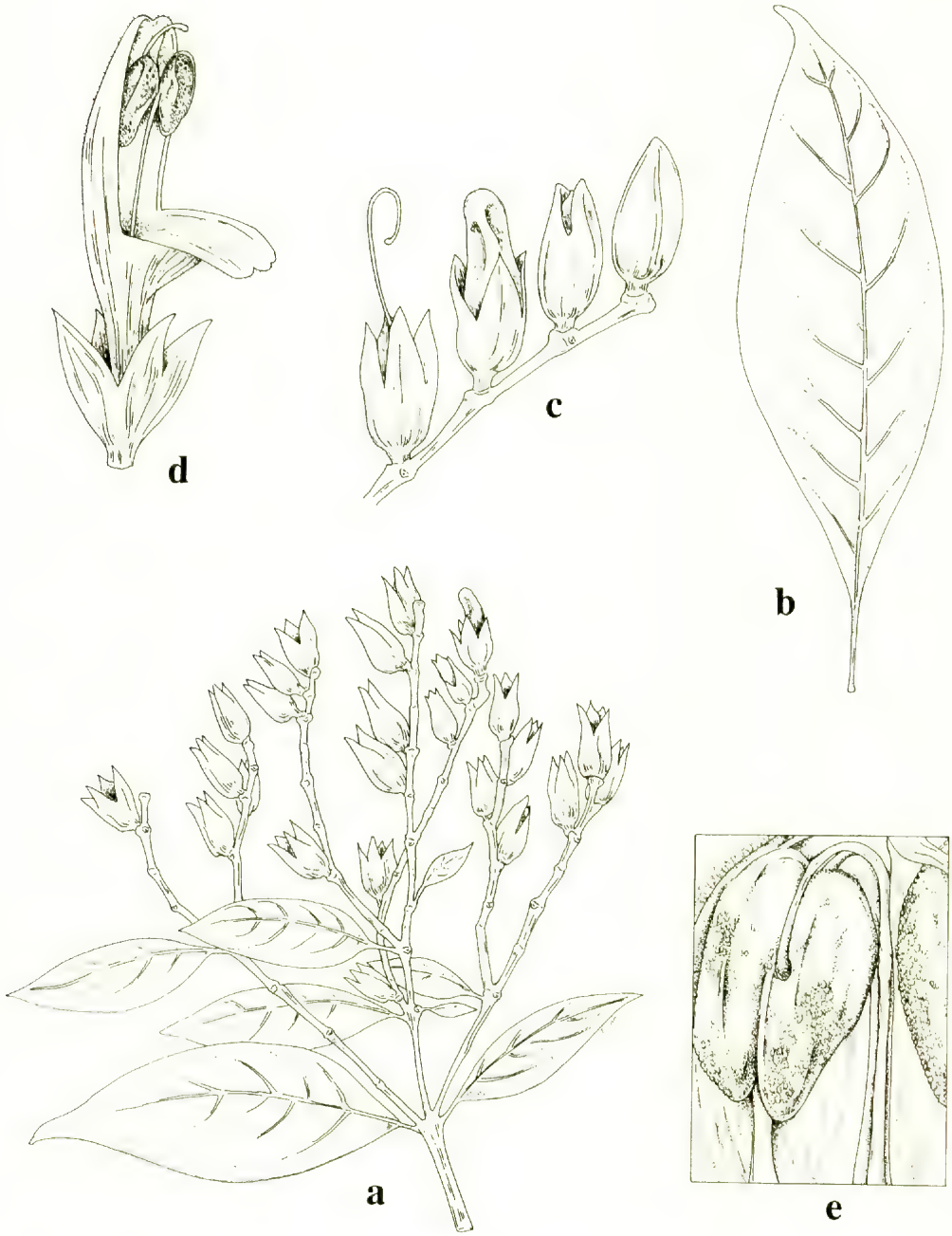

FIG. 8. *Justicia valvata*. a. Habit (*Dorantes et al. D-3538*), ×1. b. Leaf (*Vázquez T. et al. V-2582*), ×0.55. c. Portion of inflorescence with calyx in sequential stages (*Dorantes et al. D-3538*), ×2. d. Flower (*Vázquez T. et al. V-2582*), ×2.3. e. Distal portion of upper lip of corolla with stamen and style (*Vázquez T. et al. V-2582*), ×7. Drawn by Tina Cash.

Carranza, 2 km N de Poblado 2, Ejido F. J. Mina, Lat. 17°16'N, Long. 94°40'W, 25 Sep 1982, *Vázquez T. et al. V-2582* (CAS).

The likely sister species of *J. valvata* is *J. tabascina* T. F. Daniel, which occurs in similar habitats in Tabasco (Daniel 1990). Both species share the following features: caducous bracts, valvate calyces with relatively large lobes, similarly

shaped corollas with glandular pubescence, relatively large and unappendaged thecae, and 4-aperturate pollen. They may be distinguished by the following couplet:

Young stems and rachises bifariously pubescent; flowers solitary at inflorescence nodes, sessile; calyx externally glabrous. *J. valvata.*
Young stems and rachises evenly pubescent; flowers paired at inflorescence nodes, pedunculate; calyx externally pubescent. *J. tabascina.*

Some variation in pollen form was observed among the three known collections of *J. valvata*. Pollen of *Contreras 9311* from Guatemala and *Vázquez T. et al. V-2582* from Mexico (Fig. 7g–i) is virtually identical to that observed in *J. tabascina* (Daniel 1990, Fig. 2d–e). They all have well-defined insulae from near one pole to the other and a cross of polar exine separating the four bands of exine between trema regions (Fig. 7h). Pollen of the type from Mexico (Fig. 7e, f) usually has fewer discrete insulae (often only adjacent to the pores) and loops of exine not separated by a polar cross (Fig. 7f). Pollen like that of the type, in which pseudocolpi are distinct and the bands of exine between the pseudocolpi and colpi are more or less continuous or only somewhat broken up into discrete insulae, are intermediate between pollen grains typical of subtribes Justiciinae and Odontoneminae in the Justicieae.

RECONSIDERED SPECIES

Dyschoriste angustifolia (Hemsl.) Kuntze., Rev. gen. pl. 2: 485.1891. *Calophanes angustifolia* Hemsl., Biol. centr.-amer., Bot. 2: 502. 1882.—TYPE: MEXICO. See discussion for locality information, *Ghiesbreght s.n.* (holotype: K!).
Hygrophila pringlei Greenm., Proc. Amer. Acad. Arts. 41: 248. 1905. *Dyschoriste rubiginosa* Ramamoorthy & Wasshausen, Brittonia 37: 358. 1985, non *Dyschoriste pringlei* Greenm., 1904.—TYPE: MEXICO. Michoacán: hills near Uruapan, 1675 m, 13 Oct 1904, *Pringle 8847* (holotype: GH!; isotypes: CAS! UC! US!).

Ramamoorthy and Wasshausen (1985) perceptively noted that the species commonly known as *Hygrophila pringlei* properly belongs in *Dyschoriste,* and they provided the new name, *D. rubiginosa* for it. Recent botanical activities in west-central Mexico have yielded numerous collections of this red-flowered species from Colima, Jalisco, and Michoacán (Fig. 3). As a result, the geographic distribution and the morphological variability of this species are fairly well documented. Recent examination of the holotype of *D. angustifolia* revealed that it is similar in all characters to *D. rubiginosa.*

Dyschoriste angustifolia was known only from the type, a collection of A. Ghiesbreght purportedly from Oaxaca in southern Mexico (Hemsley 1882, Kobuski 1928). The holotype of *D. angustifolia* bears a printed label with the heading "Herb. Mus. Paris.," and two lines at the bottom "Mexique, Province d'Oaxaca. M. Ghiesbreght, 1842." McVaugh (1972) noted that 1842 is likely the date of receipt in Paris, not the date of collection, and that these labels were probably distributed from Paris with sets of Ghiesbreght's duplicates without an attempt to add field data to the specimens. Specimens at P commonly have additional handwritten labels with precise locality information. These reveal that plants with the printed "Oaxaca" label were sometimes collected in other Mexican states

(e.g., Morelos, Michoacán; see McVaugh 1972). At my request, Dr. Ph. Morat at P sent me photocopies of Ghiesbreght's collections of *Dyschoriste*, *Calophanes*, and *Hygrophila*. Unfortunately, none of the four specimens of which photocopies were received resemble the type at K. Three of them do have more precise locality data (e.g., "près de Cuernavaca"). A thorough search at P would undoubtedly yield an isotype of Ghiesbreght's collection. It seems probable, however, that the type of *D. angustifolia* was not collected in Oaxaca, where this conspicuous plant is not known to occur, but rather in Michoacán or adjacent regions of Colima and Jalisco, where the species is not uncommon in regions of pine and/or oak forests at elevations from 1300 to 2100 meters. It is known, for instance, that Ghiesbreght collected near Apatzingán, Michoacán (McVaugh 1972); *D. angustifolia* is known to occur near there.

Kobuski (1928) used the following combination of character states to distinguish *D. angustifolia* from all other species of the genus in his key: plants with eglandular trichomes and with stems villous-hirsute, leaves linear to linear-lanceolate and greater than 3 mm wide, inflorescences consisting of clusters of flowers at the nodes, and corollas 25–30 mm long. All of these features fall within the range of morphological variation evident among plants treated as *D. rubiginosa* by Ramamoorthy and Wasshausen (1985). The true color of the corolla of Ghiesbreght's type collection is not known with certainty. The dried corollas of the holotype are dark orange-brown. Corollas of collections identified as either *D. rubiginosa* or *Hygrophila pringlei* that did not retain their true color after drying likewise are dark orange-brown. Corollas of blue-flowered species of *Dyschoriste* that do not retain their true color after drying tend to be conspicuously lighter brown or straw colored on herbarium specimens.

Perhaps the closest relative of *Dyschoriste angustifolia*, and the only other Mexican species of the genus with reddish corollas, is *D. mcvaughii* T. F. Daniel. Distinctions between these two species were discussed by Daniel (1990).

Ruellia gooddingiana Nelson, Amer. J. Bot. 18: 437. 1931.—TYPE: MEXICO. Sonora: La Ciénega, 18 Jul 1911, *Goodding 959* (holotype: RM!).

Nelson (1931) described *R. gooddingiana* and noted a relationship with *R. tuberosa* L. He considered the possibility that his new species might be "*R. tuberosa longiflora* Gray" but noted that the former lacks the "velvety pubescence" of the latter. The only infraspecific taxon that Asa Gray described in *R. tuberosa* was *R. tuberosa* var. *occidentalis* A. Gray. It is likely that Nelson was referring to this taxon (rather than, for instance, *R. ciliosa* var. *longiflora* A. Gray), because in the protologue, Gray (1878) described the foliar vesture as "glabrate to velvety-pubescent." The type of *R. gooddingiana* was collected under mesquite in or near La Ciénega in 1911. La Ciénega is located in northwestern Sonora, approximately 150 km southwest of the international border at Nogales. Leonard (1964) did not include this name in his treatment of *Ruellia* for the Flora of the Sonoran Desert. Examination of the holotype at RM reveals this plant to belong to *R. nudiflora* (Engelm. & A. Gray) Urban, a species occurring from Arizona to Louisiana in the United States and southward throughout much of Mexico and Central America to Costa Rica (Daniel 1984a). Leaves of this specimen are sparsely pubescent to glabrate, a feature which certainly fits within the range noted by Gray (1878) for *Ruellia tuberosa* var. *occidentalis*. In fact, Gray

noted that collections from southern Arizona represented glabrate forms of the variety. Leonard (1927) included *R. tuberosa* var. *occidentalis* in *R. nudiflora* and treated the glabrate collections, including a specimen of *Goodding 959* as *R. nudiflora* var. *glabrata* Leonard. Daniel (1984a) recognized *R. nudiflora* as a variable species and listed both *R. tuberosa* var. *occidentalis* and *R. nudiflora* var. *glabrata* as synonyms. The name *R. gooddingiana* is herewith likewise included in the synonymy of *R. nudiflora*.

Ruellia rosea (Nees) Hemsl., Biol. centr.-amer., Bot. 2: 507. 1882. *Ophthalmacanthus roseus* Nees in DC., Prodr. 11: 220. 1847.—TYPE: MEXICO. Puebla: mountains near Tehuacán, 5000 ft., 1840, *Galeotti 915* (holotype: K!; isotypes: BR! LE! W!). [Homonyms: *Ruellia rosea* Mart., Obs. Mss. n. 1089, cited by Nees in Fl. Bras. 9: 61. 1847, pro syn., and DC., Prodr. 11: 215. 1847, pro syn.; *Ruellia rosea* Wall. ex Nees in DC., Prodr. 11: 177. 1847, pro syn.]

Ruellia hirsuto-glandulosa (Oerst.) Hemsl., Biol. centr.-amer., Bot. 2: 505. 1882. *Dipteracanthus hirsuto-glandulosus* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 123. 1855 (as *Diptheracanthus hirsuto-glandulosus*).—TYPE: MEXICO. Veracruz: Hacienda de Buenavista, Jun 1841, *Liebmann 10723* (lectotype, here designated: C!).

In the protologue of *Dipteracanthus hirsuto-glandulosa*, Oersted (1855: 124) cited Liebmann collections from several localities ["Paa Marker ved Hacienda de Buenaista i Dp. Vera Cruz, ved Tehuacan og S Lorenzo i Provindsen Tehuacan med Blomst og Frugt i Juni (Liebmann)"]. There are several syntypes at C annotated by Oersted with this name and with locality information corresponding to the protologue. The specimen purportedly from Veracruz is chosen as the lectotype, because it is a complete specimen with flowers and fruits, and it is the only one with a date (June) corresponding to the protologue. The syntypes from Puebla (from San Lorenzo and Tehuacán) were collected in December and May.

Hemsley (1882) indicated that *R. hirsuto-glandulosa* probably represented the same taxon as *R. rosea*. Examination of pertinent type materials bears out Hemsley's suspicion, and the former name is relegated to the synonymy of the latter. This species is distinctive among Mexican *Ruellia* by its leaves with stellate trichomes; its relatively large, purplish, and trumpet-shaped corolla; and its ± densely hirsute-glandular calyx. Pollen of the species (Fig. 2i) is typical of the genus. Although several collections from the arid Tehuacán-Cuicatlán Valley of southeastern Puebla and northwestern Oaxaca are recognizable by their longer glandular trichomes (especially on the calyx), other specimens from this region and those from Hidalgo and Querétaro with conspicuously fewer such trichomes are otherwise indistinguishable from them and are also included in this species. *Ruellia rosea* occurs, usually on limestone, in arid scrub and tropical deciduous forests at elevations from 910 to 2425 meters. It has been collected in flower and fruit from June through December. The distribution of the species is shown in Fig. 3. The lectotype locality of *R. hirsuto-glandulosa*, Hacienda de Buenavista, is located in Veracruz between Jalapa and Mirador (4 km south of Jalcomulco; see McVaugh 1987). The tropical deciduous forest in this region of Veracruz is separated from the more or less continuous arc of arid associations from Querétaro to Oaxaca (see Rzedowski 1978) from which all other collections have come.

RECENT COLLECTIONS OF LITTLE-KNOWN SPECIES

Justicia angustiflora D. Gibson, Fieldiana, Bot. 34: 66. 1972. *Beloperonides macrantha* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 162. 1855. *Beloperone macrantha* (Oerst.) Benth. ex Hemsl., Biol. centr.-amer., Bot. 2: 516. 1882, non *Justicia macrantha* Benth.,1841.—TYPE: MEXICO. Oaxaca: Trapiche de la Concepción, Dec 1842, *Liebmann 10623* (holotype: C!).

This species was originally described as *Beloperonides macrantha* Oerst., the sole species in a genus distinguished from *Justicia* and *Simonisia* Nees (=*Justicia* fide Graham 1988) by unspecified features of corolla shape, the anthers, and the inflorescence. Bentham (1876) included the genus in *Beloperone* Nees, but it was not until six years later that Hemsley (1882) effectively made the new combination for the species in that genus. Lindau (1895) also included *Beloperonides* within *Beloperone*. Gibson (1972) provided a new name for this species on transferring it to *Justicia*.

The species has hitherto been known only from collections made in Oaxaca during 1842 by Liebmann (Oersted 1855). There are Liebmann collections of *Beloperonides macrantha* at C and K. The collections at C comprise three sheets of *Liebmann 10623* from the locality cited in the protologue ("Trapiche de la Conception"). From notations on the labels, it appears that two of these were collected in December (the flowering date provided in the protologue) and one was collected in November. The collection dates at this locality do not agree with Liebmann's itinerary of 1842 as provided by McVaugh (1987). Trapiche de la Concepción, a sugar plantation and distillery located near Tepitongo, between Totontepec and Comaltepec (ca. 17°18'N, 96°?'W; McVaugh 1987), is in the Sierra Juárez, to the north and east of the city of Oaxaca. McVaugh (1987) indicated that Liebmann collected here during June and July of 1842. At K, there are two Liebmann collections labeled as *Beloperonides macrantha*, one from "Lobani," Oaxaca, and the other without a locality. Lobani (or Santa María Lovani, ca. 17°31'N, 96°06'W) is located about 23 kilometers north of the type locality. McVaugh (1987) noted that Liebmann collected in this region during June through September of 1842. At W, there is a collection referable to this species with scant label data ("Oaxaca 1842"). It likely represents a duplicate of one of Liebmann's collections. The holotype is considered to be the specimen at C with label data corresponding to the information in the protologue.

A recent collection from this same region of the Sierra Juárez (Oaxaca: Distr. Mixe, Mpio. Mixistlán, Mixistlán, 17°15'N, 96°00'W, 2 Nov 1989, *Rivera R. 1255*, CAS) is referable to this species and represents the first known collection of *J. angustiflora* in almost 150 years. Plants were collected in pine-oak forest at an elevation of 2200 meters.

Pollen of *Rivera R. 1255* matches that of *Liebmann 10623* (Fig. 7a, b; see also description below). Such pollen is not otherwise known in *Justicia*. Graham (1988) described and illustrated pollen (her "Type 9") with similar exine sculpturing but with only 2 pores (or in one case 3 pores) in some species of the American section *Plagiacanthus*. She also found intermediates between this unusual pollen type and pollen more typical of the genus. Because of insufficient material, Graham (1988) did not include *Beloperonides* in her broad concept of *Justicia*. Rather, she noted that the genus appeared closely related to *Justicia* and suggested that perhaps it

should be included within it. Given the overall gross morphological similarities of *J. angustiflora* to other species of *Justicia* and the similarities in pollen sculpturing to other species included in the genus, it would appear best to maintain this species in *Justicia*. If *Beloperonides* were to be recognized as a distinct genus, the pollen would likely be the only diagnostic characteristic for it.

The following description of *J. angustiflora* substantially amplifies upon that provided by Oersted.

Herb to 2 dm tall; younger stems subquadrate to quadrate-sulcate, bifariously pubescent with flexuose-retrorse, eglandular trichomes 0.1–0.3 mm long. Leaves subsessile to petiolate; petioles to 10 mm long; blades ovate-elliptic to elliptic, 2.3–5.5 cm long, 1.0–1.9 cm wide, 2.1–3.1 times longer than wide, acute to acuminate at apex, acute to attenuate at base, surfaces discolorous, adaxial surface dark, glabrous, abaxial surface light, pubescent along major veins with eglandular trichomes, margins flat, entire. Inflorescence of terminal, pedunculate, 2–3-flowered spikes to 25 mm long (including peduncle and excluding flowers), peduncles to 10 mm long, rachis and peduncle pubescent like young stems; flowers solitary and sessile at inflorescence nodes. Bracts (the proximalmost sometimes subfoliose) obovate-spatulate, 12–15 mm long, 3.5–5.5 mm wide, apically rounded to truncate, abaxially pubescent with straight to flexuose, glandular trichomes 0.1–0.2 mm long. Bractlets spatulate, 11–16 mm long, 2.5–3.5 mm wide, apically rounded to truncate, pubescent like bracts. Calyx 5-lobed, 8–9.5 mm long, lobes lanceolate to lance-subulate, 7.5–9 mm long, abaxially glabrous, adaxially pubescent with eglandular trichomes. Corolla pinkish purple, 48–49 mm long, externally pubescent with flexuose, eglandular trichomes 0.2–0.7 mm long, tube 25–30 mm long, upper lip 19–23 mm long, internally rugulate, apically bilobed with rounded lobes to 0.5 mm long, lower lip 18.5–22 mm long with 3 subelliptic and apically rounded lobes 4.5–7.5 mm long, 4–6 mm wide, central lobe larger than laterals. Stamens 18–20 mm long, inserted near apex of corolla tube, not exceeding upper lip of corolla, filaments glabrous, thecae superposed and suboblique, 2.5 mm long, the lower with a calcarate basal spur to 0.4 mm long; pollen (Fig. 7a, b) prolate, 4-porate, surface evenly echinate with longitudinal rows of stout spines. Style 45 mm long, glabrous; stigma subspheric, 0.2 mm long. Capsules not seen.

Phenology. Flowering: November–December.

Distribution (Fig. 3). Southern Mexico (north-central Oaxaca); in pine-oak forests; ca. 2200 m.

Specimens from Chiapas treated as *Justicia angustiflora* by Daniel (1986a) represent a similar, though distinct, undescribed species.

Pseuderanthemum pihuamoense T. F. Daniel, Madroño 31: 86. 1984.—TYPE: MEXICO. Jalisco: ca. 12–13 km SW of Pihuamo [ca. 19°15'N, 103°25'W], 19 Nov 1970, *McVaugh 24459* (holotype: MICH!).

This unusual species was described on the basis of two fruiting specimens from southeastern Jalisco (Daniel 1984b). Because corollas and stamens were not known, placement of the species in *Pseuderanthemum* was somewhat tentative. Recent collections of *P. pihuamoense* in a nearby region of Jalisco [Mpio. Zapotitlán, Lago La María, N and E sides of lake, ca. 22 km (airline) NNW of Colima in SW foothills of Volcán de Colima, 19 Mar 1991, *Sanders et al. 10697A*, UCR] and adjacent northern Colima [Mpio. Comala, Rancho El Jabali (ca. 1.5 km E of Hacienda San Antonio), ca. 4 km E of ranch headquarters, 19°26'N, 103°41'W, 20

May 1991, *Daniel et al. 6283*, CAS, K, MEXU, MICH, MO, NY, TEX, US] extend the range of the species and provide flowers for the first time. Characteristics of the corolla and androecium confirm the placement of this species in *Pseuderanthemum*. Plants at the locality in Colima were locally frequent in a cafetal with an overstory of *Fraxinus*, *Juglans*, and *Coussapoa* at an elevation of about 1300 meters. The dominant vegetation in this border region of Jalisco and Colima is mesophytic montane forest (Rzedowski & McVaugh 1966). A description of floral features that augments the other morphological information provided by Daniel (1984b) is provided below.

Corolla subsalverform, pink with white at base of central lobe of lower lip, 21–29 mm long, externally pubescent with straight to flexuose to retrorse, eglandular and glandular trichomes 0.1–0.3 mm long, tube subcylindric (somewhat hourglass-shaped, i.e., narrowest near midpoint), 15–18 mm long, limb bilabiate, upper lip 5–9.8 mm long, bilobed, lobes elliptic, 4.6–9 mm long, 2.8–4 mm wide, apically rounded, lower lip 6.5–11 mm long, trilobed, lobes elliptic, 6–10 mm long, 3–5 mm wide, apically rounded. Stamens inserted in distal 1/3 of corolla tube, included, 3 mm long, thecae 1.8–2 mm long; pollen (Fig. 2) syntricolporate, 6-pseudocolpate, the 2 pseudocolpi in each mesocolpium fused into a pseudocolpal ellipse, surface reticulate; staminodes 2, 1.3 mm long. Style included, 10–14 mm long, glabrous; stigma 0.5 mm long, unequally bilobed.

This species, which was last collected by McVaugh in 1970, is perhaps not as rare as suggested by the few known collections. In northern Colima, plants occur in a disturbed habitat (i.e., a coffee plantation with the native overstory intact) with at least one other rarely collected, but widely distributed, species of Acanthaceae (i.e., *Dicliptera nervata* Greenm.). The practice of preserving most, or at least some, of the native overstory trees in coffee plantations has the ecological advantage of preserving part of the natural biological community. In addition to the many epiphytes in the overstory trees, those native understory herbs and shrubs that can tolerate some disturbance often persist as well.

Tetramerium guerrerense T. F. Daniel, Syst. Bot. Monogr. 12: 101. 1986.—TYPE: MEXICO. Guerrero: Distr. Galeana, Atoyac, 3 Dec 1937, *Hinton et al. 11000* (holotype: GH!; isotypes: ENCB! LL! MICH! NY! RSA! UC! US!).

This species was based solely on the type collection from seaward slopes of the Sierra Madre Sur near Atoyac, Guerrero (Daniel 1986b). A recent collection of *T. guerrerense* from a nearby region in Guerrero (Mpio. Atoyac, between Atoyac and Puerto del Gallo, 6.4 km NE of Los Parotas, 6 Jan 1990, *Daniel & Ton 6142*, CAS, DUKE, ENCB, K, MEXU, MICH, MO, NY) represents the second known collection of this species. The latter collection was made in a region of tropical subdeciduous forest at an elevation of 275 meters. In morphological features, plants from the recent collection do not significantly alter the description provided by Daniel (1986b). Fifty-three years since it was last collected in the region, *T. guerrerense* still persists in the dry forests of west-central Guerrero.

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A LICHENOLOGIST'S VIEW OF LICHEN MANNA

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Out of biblical tradition the word manna carries with it a connotation of the unexpected and providential, a food miraculously provided in times of dire need or a spiritual nutriment, a bread of angels. But in the literature of the past two millenia, it has also been applied to a great number of foodstuffs and medicines of a varied vegetal origin. It is said that the children of Israel, facing starvation in the wilderness of Sinai, were astonished to find a food rained from heaven and exclaimed *mân-hû*, what is it? ("for they wist not what is was"). That is the origin of the word, as recorded in the book of *Exodus*, and from that source the word passed with little change into Arabic, Greek, Latin, and many modern European tongues. However, an alternate explanation is that the Arabic *mann* means a gift or a gift from God, and the Israelites may have taken that word from the people indigenous to the Sinai. And they in turn may have borrowed the word from the Sumerian *ma-nu*, the name given to a tree sacred to a sky god and persistently associated with the date palm and the tamarisk, both sources of sweet manna substances.

The word manna has been used especially for substances that cover the ground or desert trees and shrubs and thus seem to have fallen from heaven. Most of the so-called mannas are Middle Eastern, but the word has also been used for plant products from many other parts of the world. Harrison, in 1951, enumerated genera belonging to 19 families of angiosperms in addition to several gymnosperms and a few fungi, including lichens, as types of manna. In his book, *Manna: An Historical Geography*, published in 1980, Donkin provided an erudite treatment of the subject, based on a literature of 982 titles from Herodotus onward (and fortified with 763 footnotes). De Visiani, in 1867, presented an particularly interesting and detailed account of a lichen, *Lecanora esculenta*, thought to be the manna of the Hebrews, and the subject of biblical manna was also explored, in 1952, by the Moldenkes in their *Plants of the Bible*. My knowledge of the subject is derived from those and numerous other sources as well as my own observations on *Lecanora esculenta* in the Libyan desert during the winter of 1980 and 1981.

It is, of course, futile to seek a botanical explanation for the God-given, and the difficulties of identifying a plant product from an ancient, hearsay, polyglot literature is compounded by a common tendency to exaggerate the highly prized and seemingly miraculous. The manna plants described in the Arab literature include especially desert scrubs referable to *Tamarix* and *Alhagi*. This kind of manna can be narrowed down to sweet exudates from leaves and branches as well as honeydew drippings from insects living on them. For the most part, the literature gives no means of distinguishing the one from the other. However, de Visiani, in 1867, reported that a scale insect was instrumental in producing the sweet exudate of *Tamarix mannifera*, and investigations in the Sinai, reported by Bodenheimer as recently as 1947, have demonstrated that scale insects suck fluid from

the phloem of at least one species of *Tamarix* and excrete it as a honeydew. Such exudates, whether plant or animal in origin, were highly prized in times gone by when desert peoples depended on honey, date syrup, and grape juice for a scant and uncertain supply of sweets.

In the books of *Exodus* and *Numbers* the manna that sustained the Israelites was described as a small, round thing, as small as hoar frost on the ground, resembling coriander seed and white (or pearly white like "bdellium") and when baked tasting like fresh oil or wafers made with honey. It appeared with the morning dew, but during the heat of the day it bred worms and stank. If it is at all reasonable to search for an identifiable manna rather than a miraculous bread from Heaven, are there plant products of the desert that conform to such a description and could conceivably appear unexpectedly in huge quantities, day after day, year after year? It has been estimated that upwards of 2,000,000 Israelites depended on a daily supply of manna over a period of 40 years. Based on a daily allowance to each person of about one pound, the total requirement would be about 1000 tons each day (not to mention the amount needed for flocks of sheep and goats). Is it likely that any of the manna plants singled out from the literature would have provided a dietary balance and palatability acceptable to a people prone to "murmur" in the face of adversity?

Explanations of biblical manna can be sorted out into four categories:

1. *Exudates from desert trees and shrubs.* These substances have figured consistently in the Arab literature on manna. In the apocryphal book of *Baruch*, a manna was mentioned long after the exodus: "Behold, we have sent you money to buy burnt offerings, and sin offerings, and incense, and prepare ye manna, and offer upon the altar of the Lord our God." This kind of manna, apparently available for purchase, the Moldenkes attributed to exudates from *Tamarix mannifera*, *Alhagi maurorum*, and *Fraxinus ornans*. Sweetness dripping from the leaves and branches of *Tamarix* and *Alhagi* hardens on drying and is collected, even now, by shaking over a cloth spread. The *Fraxinus*, or manna ash, provides an exudate used as a laxative and demulcent that is tapped from trees in the Mediterranean area (especially in Sicily) by making incisions in the bark. Both in terms of quantities available and suitability as food, the exudate mannas can scarcely be accepted as the kind provided by God for the good of his people.

2. *Something that grew up at night but withered away and stank in the heat of the day.* In India and China, gelatinous crusts of *Nostoc*, a blue-green alga, have been gathered from the soil and used as desperation food. Such a food may have been available to the Israelites, but in a desert land certainly not in quantity. Swann, in his *Fighting the Slave-Hunters in Central Africa*, told of seeing a curious white substance similar to porridge covering the ground in the high plateau that separates Lakes Nyasa and Tanganyika. "It was found early in the morning before the sun rose. On examination it was found to possess all the characteristics of the manna...of the Israelites. In appearance it resembled coriander seed, was white in colour like hoar frost, sweet to the taste, melted in the sun and if kept over night was full of worms in the morning. It required to be baked if you intended to keep it for any length of time. It looked as if it had been deposited on the ground in the night. The only suggestion I could think of was that it might be a mushroom spawn, as on the spot where it melted, tiny fungi sprung up the next night." Harrison too mentioned fungi as closer to the biblical description of manna.

However, the nutritive value of such fungi would be minimal, and one would scarcely expect a sustained abundance of fungi in the desert.

3. *The meat and dung of migratory birds.* We can surely discount a suggestion that the manna that appeared so suddenly and in such quantity consisted of the meat and dung of a quail (*Coturnix coturnix*) that breeds in Europe and the Middle East and winters in Africa. Aided by favorable winds, these birds often arrive in vast numbers during a single night. In the Bible, quail are mentioned as arriving in the evening and the manna the following morning, but the Hebrew word for the bird is not at all like that for manna, and there is no reason to think that the children of Israel were not familiar with the bird or associated it in any way with manna. If their manna had been that bird, however tasty, or its dung, however nutritious, there would have been no sense of the miraculous, nor would such a manna have been available throughout the year.

It is perhaps coincidental that the so-called manna lichen, *Lecanora esculenta*, was known as pigeon's dung in the area of the Euphrates (according to a writer of the twelfth century, Ibn al-Baitar). Such a name in still more ancient times might explain a reference in the second book of *Kings* to a famine in Samaria, where the fourth part of a cab of doves' dung sold for five pieces of silver. This lichen, indeed edible, does not occur in Samaria now, and there is no reason to think that it did in the past. However, it could have been available for purchase.

4. *A bread rained from Heaven, possibly an airborne lichen.* According to the Moldenkes, "the manna that fell so regularly from the skies was in major part, at least, composed of several lichens, *Lecanora affinis*, *L. esculenta*, and *L. fruticulosa*. These species after long periods of drought curl up and break loose from the ground. Being extremely light, they are often transported great distances in the air, ultimately falling to the ground again and sometimes forming layers several inches deep. Often these lichens fall in places where they are unknown to the natives in any state except that in which they find them after they have dropped so mysteriously from the skies" [quotation somewhat abridged]. The Moldenkes thought that drippings from desert scrubs, together with the meat and dung of quail, may have supplemented a lichen diet and that biblical manna can be interpreted as a combination of foodstuffs rather than a single plant product.

The lichen manna is scarcely likely to have sustained a host of people over a long period of time. Those lichens mentioned by the Moldenkes have indeed served as starvation food. It is said that inhabitants of Sistan, in eastern Persia, preserve a tradition that part of Alexander's army, in 330-327 B.C., was saved from starvation by using *Lecanora esculenta* as a food. The lichen is reported to accumulate suddenly and in quantity as a result of violent wind storms. Lichen rains were reported in 1824, 1828, 1829, 1846, and 1890 in central Turkey, Armenia, and northern Persia, in some cases in areas gripped by famine. Although the lichen was said to be unfamiliar to residents of those areas, it seems likely, if not probable, that it may have gone unnoticed except in times of dire need.

The suggestion that unattached desert lichens may have been available to the Israelites as a miracle food is, in fact, no more than a pious conceit of Victorian times. Such vagabond lichens have never been recorded from the Sinai, and it is unlikely that large quantities of the lichen were continuously blown in from a distance over a period of 40 years. Furthermore, the medieval writers of Islam's

FIGS. a–c. Habitats occupied by the manna lichen, *Aspicilia esculenta*. a. A typical rocky habitat with very few shrubs at the Wadi Al Masus area south of the Haruba Project. The lichen forms an almost continuous cover where larger, darker sheep dung can also be seen. The annual precipitation at this spot is less than 50 mm. The Bedouin was among a number of people who accompanied me to this spot. b. Khalifa Danhus, who served as my companion on several excursions, is standing in a typical rocky expanse in the Wadi Al Masus area south of the Haruba project. The lichen can be seen as a darkness scattered among the rocks. c. Mohamed Araby, who guided me to the *Aspicilia* barrens of the Hamada al Hamra, had himself taken flocks to that area.

golden age of science made no mention of lichens as a famine food, nor did they confuse them with the sweet mannas. (The earliest mentions of the lichen appeared in Arabic works of the ninth to thirteenth centuries and only as an ingredient of a wine made from honey and of medicinal compounds.) The children of Israel murmured, "But now our soul is dried away; there is nothing at all, beside this manna, before our eyes." They would indeed have complained if the diet had been restricted to a tasteless and possibly indigestible lichen. Neither the people nor their animals could have survived on such a singularly unbalanced diet.

Lecanora esculenta and its relatives can be considered no more than a wretched starvation food. No one who has tasted it, as I have, would think of it in any other way. It is tasteless, unless faintly mushroomlike. I was told that the lichen takes on a sourness later in the season, but I see no reason why that should be. It surely would not taste like fresh oil or wafers made with honey when baked. In the steppes of the southern "USSR," *Lecanora esculenta* has been mixed with flour and made into bread. In North Africa, it has also been used, very exceptionally, as an ingredient of bread or eaten as it occurs in nature or parched with or without oil. I encountered no one in Libya who had actually eaten the lichen, although one person told me that his father had depended on it as food during internment

FIGS. d–g. d, e. *Aspicilia esculenta* spread over the ground and accumulated at the base of bushes at Ajarmia in the Wadi al Masus area south of the Wadi al Bab project. f. A flock of sheep grazing on *Aspicilia esculenta* at Ajarmia. Goats are rarely seen in Libya. Because they crop vegetation too close to the soil and increase the possibility of erosion and gulley washing, they are actually outlawed. g. Donkey used by the Sudanese shepherd as a pack animal. He is standing among the *Aspicilia* and presumably eating it, as nearby sheep are.

by the Italians early in the Second World War. As recorded by de Visiani, in 1867, during the French campaign in Algeria, around 1845, a General Jussuf found that mixing the lichen with a one-tenth portion of flour made a bread of acceptable texture and taste. He fed his horses a lichen-barley mix for several weeks with no ill effects and said that camels, gazelles, and other quadripeds eat the lichen.

Libyan sheep herders normally take their flocks to lichen feeding grounds only in times of severe drought. Where it grows in abundance (figs. a–c, d–g), the lichen is conspicuous even from a motor vehicle traveling at relatively high speeds, but leading a flock to it requires a landmark visible from afar. In eastern Libya, at least, shepherds erect cairns so that good pasturage can be relocated. I was told by persons of the Libyan department of agriculture that they became interested in using the lichen as forage and perhaps putting it into cultivation in a particularly dry year in the seventies when it was reported that sheep were being taken to the desert to graze on *torba*, or soil. Some of them thought of the *torba* literally as soil, but others did know about the lichen and its potential use in forage. I interviewed shepherds who knew the lichen "torba" and where to find it. They sometimes rake or sweep up quantities of the lichen and haul it by truck to places where water is more readily available. However, in 1980 and 1981, when I was there, the Libyan government was sending water to the desert in what appeared to be oil tankers to supply flocks grazing on the lichen. I saw three wells with generators, and watering troughs that had recently been installed in the barren

Hamada al Hamra where the lichen was abundant. (I was told that sheep can go three days without watering during the winter, but only one day in the summer.)

Notes accompanying a Libyan collection made by Robert Sweet in 1959 refer to the lichen as "trub," a substance well known to the Bedouin sheep herders who insist that this and water are sufficient food for sheep or goats. At this locality, about 30 km west of Tongeder, the lichen is found in abundance over an area of 10 by 3 km, and it is possible to harvest a one-pound coffee can full from an area two feet square. "We heard from Bedouins in the desert that a ewe can drop a lamb and produce a good market product in four months on this alone; it tends to bloat; the Bedouins, while investigating their camels in the desert, often sack and bring trub to their sheep that are on other ranges; and if a ewe is grazed on this area longer than three summers all of her upper lip with be gone, and she will be of no value (probably from picking it from the rocks)."

Goebel, in 1830, reported the starch content of *Lecanora esculenta* to be 23% of the dry weight with most of the remainder, 66%, made up of calcium oxalate. Other analyses have shown 11% lichen starch, or lichenin, and 60% calcium oxalate. I was told that a lamb weakened by hunger or a flock in a sick or rundown condition could be fattened up and restored to health after a week's diet of lichen. However, it was said that sheep need carotene, or vitamin A, from other plants in order to digest the lichen well and that the lichen causes "stomach trouble" unless given with a food supplement such as mash. Renard and Lacour, in 1880, quoted reports that in Algeria the lichen was regarded as poisonous and that shepherds were quick to sell animals that had eaten it. My Libyan informants said that two teams of veterinarians studied a disease among lichen-fed sheep in the Hamada during the particularly dry summer of 1977 and that the disease has since spread to other areas and become epidemic. The disease, eventually ending in death, is manifested by whitish salivary drooling, distended blood vessels, and spurting blood (on slaughtering). Whether a lichen diet would cause an epidemic seems doubtful, but a food almost entirely lacking in fats, proteins, and minerals and carrying a heavy burden of calcium oxalate would seem unsuitable for man or beast. It may be that in combination with the acidity of the stomach calcium oxalate causes trouble even though its solubility in water is too low to affect palatability. A heavy diet of a relatively insoluble and indigestible starch would be particularly troublesome in times of water shortage. Lichen starch is the chief component of lichen cell walls. It is a derivative of galactose and occurs in the form of two isomeres: The form found in *Lecanora esculenta*, lichenin, is soluble in hot water, whereas isolichenin dissolves in cold water (and stains blue with iodine).

According to Libyans involved in range management, shrubs rooted in a caliche soil are salty, and sheep and goats graze on them only after a rain or during a morning fog when the salt is washed down or diluted. During the heat of the day, they prefer lichens, but if winter annuals are available they will shun both shrubs and the lichens. That grazing animals indeed eat lichens by preference seems demonstrated by the dung seen where lichens were used for forage. The fine-textured dung of animals eating only the *Lecanora* was much more common in the lichen barrens than fibrous dung resulting from a more varied diet.

It appears that lichen starch (whether lichenin or isolichenin) is readily digested by ruminants, but humans may digest it less well, or perhaps, not at all. The caribou of the American arctic are said to derive 95% of their winter diet from macrolichens, and in northern Scandinavia similar lichens are fed to grazing animals

as hay or ensilage (after being soaked in a weak solution of potassium carbonate, presumably to leach out some bitterness). In Sweden and Iceland lichens have been mixed with grain to make a bread flour and also used to thicken soups and puddings. Eskimos eat very little vegetable matter but enjoy the lichen-filled paunch of the caribou, perhaps as a pre-digested source of vitamins.

It has been reported that *Lecanora esculenta* can be carried long distances by high winds and flash floods and accumulate in windrows as much as 20 or 30 cm deep. There have been no reports of lichen rains in North Africa, and no one that I talked to in Libya knew of lichen rains even during the violent wind storms of July and August or had seen *Lecanora* accumulated in windrows. I observed that during strong gusts of winter wind the air seemed quiet at ground level. The lichen thalli merely quivered, and they were often slightly embedded in the silty soil. I saw the lichen rather uniformly spread out over vast areas, regardless of the force of the wind, and the only accumulations I saw were in the vicinity of shrubs or other wind barriers, but in no significant quantity (figs. d, e). A greater displacement of thalli may occur during summer winds, but even then the meager cover of shrubs and rocks studding the sandy flats in which the lichen occurs would probably block wind movement at ground level and make long distance transport no more than a remote possibility. A range manager who had observed the lichen in the Wadi al Masus area of eastern Libya for the past 16 years told me that the area occupied by the lichen had not expanded and that a fairly continuous cover had been maintained throughout that time, regardless of the season.

Al-Bakri recorded, in the eleventh century, that in Cyrenaica a soil, or *torba*, is mixed with honey and fermented as a drink. This *torba* can be identified with *Lecanora esculenta*, a pinkish tawny lichen that somewhat resembles the soil on which it grows, generally unattached, but sometimes adherent to rocks. It grows in eastern Libya (Cyrenaica) in the Wadi al Masus area and also in the west (Tripolitania) most extensively in the vast plateau Hamada al Hamra. In the Wadi al Masus region the lichen is abundant over an area 70 km long and 30 km wide, and it is said to be equally common, over an even greater area in the Hamada. The lichen was recorded in Keith's *Libyan Flora* from Tarhunah, Cabas, Bir Alleg, and Gharian, all in western Libya. I found it very sparsely at the Oshtada Project near Tarhunah. The director of that project told me that he had seen it 20 years earlier, about 1960, in the vicinity of Cabas. I saw it in that same general area, in the Wahsa plain between Jadu and the Hamada al Hamra. It is not to be found at Bir al Granam, which is near Bir Alleg, according to my own observations and the word of local shepherds. I did not see it at or near Gharian, which lies in an area of rugged topography not at all similar to the windswept flats favored by the lichen.

My observations and collections were made at (1) Ajarmia, in the Wadi al Masus area, 77 km S of the Wadi al Bab Project, December 28, 1980; (2) Wadi al Masus area, 55 km S of the Haruba Project, January 7, 1981; (3) Hamada al Hamra, 160 km S of Jadu, January 2, 1981; (4) Wahsa plain, 44 km S of Jadu, January 2, 1981 (5) Wahsa Plain, 51 km S of Jadu, January 2, 1981; and (6) Oshtada Project, 53 km S of Tarhunah, December 31, 1980.

The optimal habitat (figs. a–c) for the lichen seemed much the same in both the eastern and western regions of Libya. Windswept flatlands support a sparse cover of low shrubs spaced no closer than 30 feet apart and reaching a height of only about 1.5 feet. In the summer it is very hot, dry, and windy. In the winter, it

is also windy but cold, often foggy in the morning and overcast during the day, with precipitation varying from two to five inches per year (or perhaps less). The soil, studded with limestone rocks and pebbles and low outcropping ridges, is fine-grained, neither a silt nor a sand but somewhere in between. It is a caliche soil with crystals of calcium sulfate or calcium magnesium sulfate at or near the surface. The caliche nature of the soil is evidenced by the kind of vegetation and also by the fact that water-catching shrubs are conspicuously ringed by a soil darkened by mineral salts continually brought to the surface owing to shallow penetration of water and rapid evaporation. By far the most common shrub is *Anabasis articulata*, but *Halixylon*, *Artemisia*, *Salsola*, *Suaeda*, *Salicornia*, and *Atriplex* are also present. The annual herbs had not begun growth when I was there, in late December and early January, but remains of *Stipa*, *Trifolium*, and *Plantago* could be seen. The lichen covered large areas interspersed with bare spots where neither lichens nor ephemeral herbs grew, often in places with few pebbles and rocks where water stands after a rain. Areas of better drainage and soils stabilized by wind-breaking rocks or shrubs favored the lichen. Very similar *Anabasis-Artemisia* steppe habitats were photographed and described by Keller (1930) as favorable to *Lecanora esculenta* and its relatives in the Urals and lower reaches of the Volga. *Lecanora* (*Aspicilia*) *esculenta* is reported to occur in Algeria and Libya and, disjunctively, in Greece, Turkey, Iran, southern Russia, and southwestern Asia. I have been able to confirm the distribution only in part (see below). The actual distribution is difficult to determine from the literature because of confusion with other gypsy lichens of some similarity.

Elenkin, early in the present century, recognized seven forms of a single species, *Aspicilia alpino-desertorum*: four of them alpine at altitudes up to 12,000 feet (*esculenta-alpina*, *affinis*, *fruticulosa*, and *fruticulosa-foliacea*); three of them in steppes and deserts at lower altitudes (*desertoides*, *foliacea*, and *esculenta-tesquina*). The globose forms *esculenta-alpina*, *affinis, fruticulosa*, and *fruticulosa-foliacea* he derived from the crustose *Aspicilia desertorum*. In his opinion, the *esculenta-alpina* form gives rise in steppes and deserts to the crustose *desertoides*, from which the lobulate-foliose *foliacea* is derived. The latter, in turn, gives rise to the *esculenta-tesquina* variant (as represented in Libya), differing from the *esculenta-alpina* expression in its more angled contours and marbled interior (figs. j, k). It is obvious, however, that these seven expressions can scarcely be retained in a single species, and their relationships to one another are not at all convincing. Zahlbruckner, in *Die natürlichen Pflanzenfamilien*, recognized only three species, as *Lecanora esculenta*, *L. fruticulosa*, and L. *affinis*. (For nomenclatural reasons, *L. affinis* is better called *L. vagans*.)

Lecanora, in a traditional sense, is a very large and inclusive genus. Most of its species form crusts on rocks or bark of trees. However, some members of the section *Aspicilia* may begin growth as crusts that tend to get humped up as excrescences and eventually freed from a rocky substrate, perhaps as a result of differing rates of growth associated with an alternation of summer drought and winter wetness. The detached form, continually shifting in position, loses dorsiventrality and develops an algal layer on all sides. In the rocky areas of Libya where *Lecanora esculenta* is common, it is difficult to find the crustose phase of growth, but some evidence of thalli detaching themselves from the substrate was seen (figs. h, i).

In recent years, lichenologists have recognized *Aspicilia* as a genus rather than a section of *Lecanora* and assigned it to the family Aspiciliaceae rather than

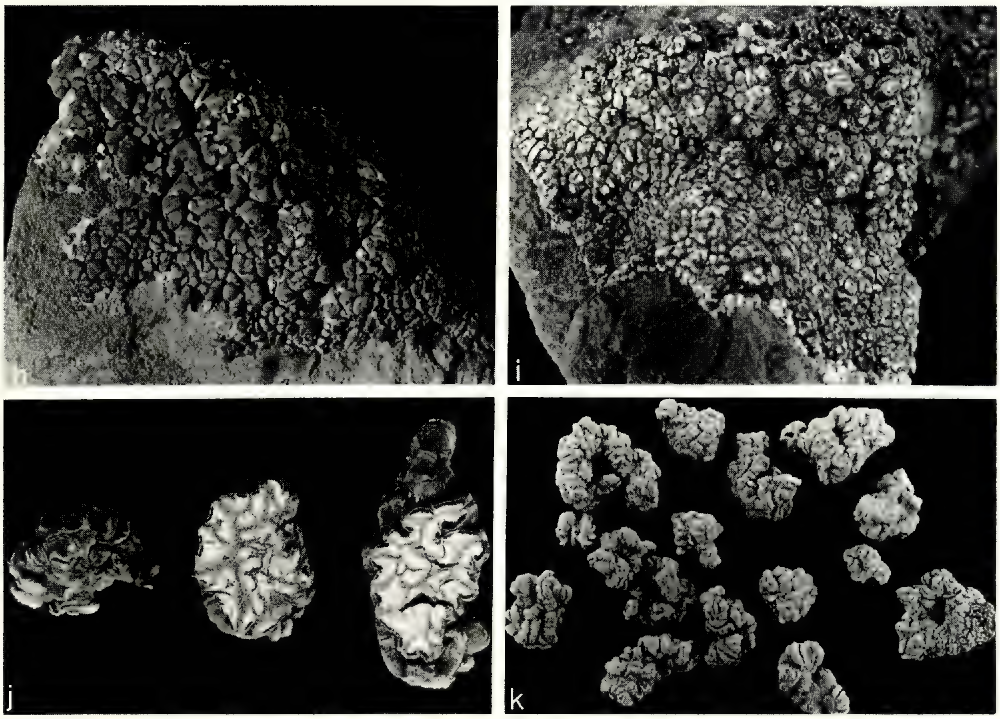


FIG. h–k. h–i. *Aspicilia esculenta* is only occasionally seen attached to rocks. In both figures, the tendency for portions to hump up and free themselves from the substrate can be seen. j. Free-living thalli of *Aspicilia esculenta* showing variations in size and form. The thalli are more or less rounded in outline but somewhat flattened. k. Free-living thalli of *Aspicilia*; the two on the right are shown in section. The alga layer is shown as arcs of dark green in depressions on all sides of the convoluted thallus. The medulla is white marbled with brown.

the Lecanoraceae. This seems reasonable to me, or at least a step in the right direction, even though the genus *Aspicilia* is hard to define. The form of the thallus ranges from crustose to coralloid, subfruticose, and lobed-foliose. The species that we are concerned with, of the *A. alpino-desertorum* group, have a reduced number of spores per ascus, and the spores are relatively large, thin-walled, and colorless. As discussed by Hafellner, 1991, *Lecanora*, in a broad sense, shows three lines of chemical divergence: *Lecanora* characterized by atranorin, *Placodium* by usnic acid, and *Aspicilia* by norstictic acid (Follmann & Huneck, 1968b, 1969). Actually, most species of *Aspicilia* produce no lichen substances at all, but Follmann and Huneck (1968a) found stictic acid in *A. jussufii* (positive with paraphenylene diamine and identified by thin-layer chromatography), but found no lichen acids in six other species of the *A. alpino-desertorum* complex (*A. affinis, A. aspera, A. esculenta, A. fruticulosa, A. lacunosa*, and *A. terrestris)*. I have been unable to demonstrate lecanoric acid (so commonly produced by *Lecanora* species) or any other lichen substance in Libyan material of *Aspicilia esculenta*, by spot test with C and K, crystalline tests, or thin-layer chromatography (using toluene 180: dioxane 45: acetic acid 5). The algal layer tests blackish purple with iodine (indicative of a green algal symbiont), but the medulla is negative (owing to lichenin rather than isolichenin).

The families and genera of lichens are defined, to an extent at least, on fungal characteristics, although the form and chemistry of the thallus may provide addi-

tional distinctions. Fungal spores are incapable of producing a lichen, except by chance encounter with an appropriate alga, and the chances of fungal and algal symbionts getting together scarcely exist in the harsh environments in which lichens grow. Many lichens reproduce mainly or even exclusively by vegetative means. *Aspicilia esculenta* seldom produces apothecia or spores, and reproduction very likely results, as in most lichens, from fragmentation and regeneration. I saw considerable evidence of such fragmentation, probably resulting from abrasions associated with a tumbleweed existence and the trampling of grazing animals. The soil of the Libyan desert is easily blown in the summer but compacted in the winter because of a small particulate size and the binding effect of a calcium carbonate and calcium magnesium sulfate content. In the winter wetness, lichen thalli and fragments often become partially buried, and such an intimate contact with moist soil during the only season conducive to growth no doubt aids in regeneration.

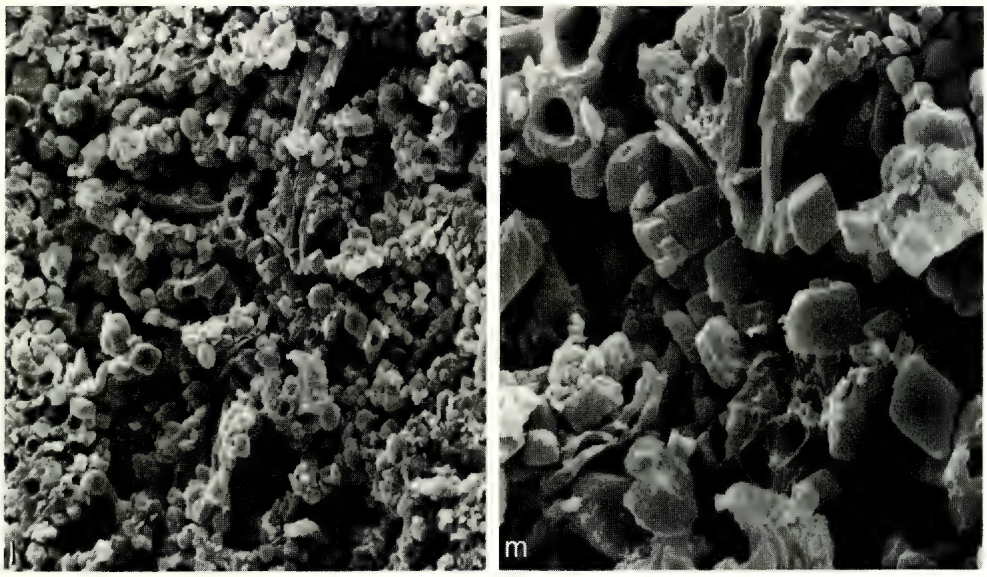
The apothecia of *Aspicilia esculenta* are somewhat immersed owing to an upgrowth of surrounding thallus tissue. The asci contain four (or exceptionally three or five) rounded-ellipsoidal, colorless, 1-celled spores measuring 19.1–19.4 μm in diameter. Similar apothecia but no spores were seen in specimens of *A. fruticulosa* and *A. jussufii*, but no reproductive structures were seen in *A. vagans*.

The thallus of *Aspicilia esculenta* is encrusted with crystals of calcium oxalate at the outer surface and the surface of medullary hyphae. It appears that oxalic acid secreted by the fungal hyphae causes calcium oxalate to be formed as an insoluble extracellular deposit. The crystals of calcium oxalate can be needlelike raphides, imparting a tingling taste to many of the Araceae, such as the Indian Turnip, as *Arisaema* tubers are often called, or short rhomboids as in the *Aspicilia* (figs. l, m), apparently depending on how they are "seeded." (Similar photographs of calcium oxalate crystals of a rhomboidal form are presented by Jones, 1988.) The acid taste of oxalic acid, associated with the raphide form of crystal, could not be detected in *Aspicilia esculenta*.

As the accompanying illustrations (figs. n–s) show, at least four species persistently referred to *Aspicilia esculenta* can be recognized as perfectly distinct. I can partially confirm the ranges of distribution of those species and some other members of the *A. alpino-desertorum* complex based on specimens at the University of Michigan, the New York Botanical Garden, and the Farlow Herbarium of Harvard University, as follows:

Aspicilia esculenta (Pall.) Flag. [*Lecanora esculenta* (Pall.) Eversm.]: LIBYA: Hamada al Hamra and the Wadi al Masus area south of Wadi al Bab and also south of Haruba). USSR: Astrakhan, Uralsk, vicinity of the Don River, and Kirgiz Steppes (central Kazakh S.S.R.).—The thalli are relatively large and coarse, rounded in outline, slightly flattened, convolute-wrinkled, and essentially lacking pseudocyphellae. Figs. r, s.

Aspicilia jussufii (Link) Mereschk. [*Lecanora esculenta* var. *jussufii* (Link) Stein.; *L. jussufii* (Link) Follmann & Huneck, comb. illeg.]: ALGERIA: from the "Sahara" and from Laghouat, in the Atlas Mountains. LIBYA: Hamada al Hamra and south of Jadu in western Libya and the Wadi Masus area south of Haruba in eastern Lybia.—This species is distinct from *A. esculenta* in its much smaller, nodular form, numerous pseudocyphellae dotting each areole, and content of stictic acid. (Algerian specimens have a dull reddish color, perhaps because of age.) I have not determined whether



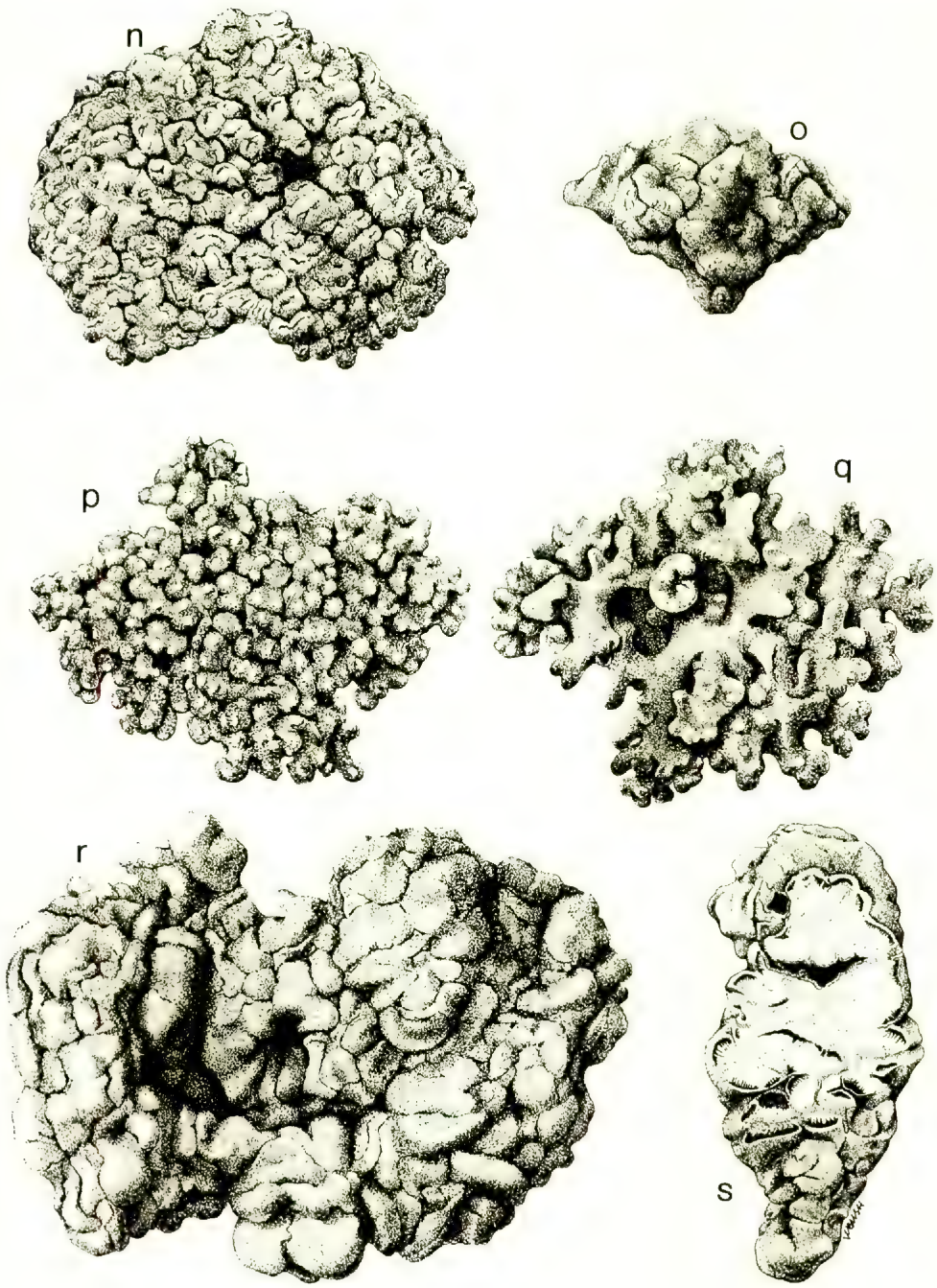
FIGS. l, m. SEM photographs of sections through the medulla of *Aspicilia esculenta* showing fungal hyphae and a large number of rhomboidal crystals, presumably of calcium oxalate. The magnifications are ×375 and ×750. (SEM photographs supplied by P. Dayanandan.)

this is the same as *A. tominii* Oxn. (*A. esculenta* var. *altaica* Tomin), as an illustration in the *Handbook of Lichens of the USSR*, vol. 1, p. 197, suggests. Fig. o.

Aspicilia vagans Oxn. [*Lecanora affinis* Eversm.]: USSR: Astrakhan, vicinity of the Don River, the Altai, "in deserto Czuensi," and the Kirghis Steppes (central Kazakh S.S.R.). IRAN: at the Russian border at Aschabad. SPAIN: Sierra de la Costera, near Cañada Vellida, *Follmann & Follmann-Schrag* (NY, as *Sphaerothallia fruticulosa*).—This lichen is smaller and more globose than *A. esculenta,* irregularly papillate at the surface, with papillae unbranched and pseudocyphellae rather few). Fig. n.

Aspicilia fruticulosa (Eversm.) Flag. [*Lecanora fruticulosa* Eversm.]: USSR: Astrakhan, vicinity of the Volga River and the Kirghis Steppes (central Kazakh S.S.R.). SPAIN: Paramera, prov. Soria (distributed as Vezda, *Lichenes Selecti Exsiccati 1904*, as *Sphaerothallia fruticulosa.—Aspicilia fruticulosa* is similar to *A. vagans* but more nearly fruticose in being branched above a point of attachment and having papillae forked and pseudocyphellae usually single. Elenkin attributed the forked papillae of *A. fruticulosa* to relatively moist conditions of growth, but I have seen no intermediates between it and *A. vagans*. Figs. p, q.

Aspicilia aspera (Mereschk.) Tomin [*Lecanora desertorum* var. *aspera* Mereschk.]: USSR: Astrakhan.—This is a coarse and indeterminate excrescence loosely attached to the soil and somewhat papillate as well as folded. Its appearance approaches that of *A. esculenta* and *A. vagans*, but it seems to retain its dorsiventrality. It has also been called *A. alpino-desertorum* f. *fragilis* Elenk., perhaps in reference to a loose, irregular, and seemingly fragile growth form.



FIGS. n–s. Species often referred to as lichen manna and commonly lumped together as *Aspicilia esculenta*. n. *A. vagans* (*Lecanora affinis*). o. *A. jussufii*. p, q. Top and bottom views (showing the point of attachment) of *A. fruticulosa*. r, s. Top and cross-sectional views of *A. esculenta*. (Drawings by Lisa Bush.)

Aspicilia lacunosa Mereschk.—I have seen no material, but the type of *Lecanora (Aspicilia) lacunosa* Zschacke from Monte Angelo, Corsica (FH), is a dark crust with small, crowded areoles and abundant apothecia having the hymenium largely exposed. It has the appearance of an *Acarospora* and is not at all related to the vagabond species of *Aspicilia*.

Aspicilia desertorum (Krempelh.) Mereschk.—USSR: Astrakhan. This is a crust growing on rock with numerous apothecia, of which the hymenium is largely exposed and surrounded by a heavy thalline exciple. Contrary to Elenkin's views, it does not seem particularly like the vagabond members of *Aspicilia*, and there seems no obvious reason to think of it as giving rise to any member of the *A. alpino-desertorum* complex (or any convincing reason to think of that complex as a natural one).

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I visited Libya at the invitation of the Libyan Secretariat of Agriculture. I was provided with hospitality and given the opportunity to make observations under the guidance of persons knowledgable in range management. Ali Ramadan, Director General of Agricultural Research and Education, deserves special mention, as do Mohamed Soghmari, Khalifa Danhus, Rajab Mohamed El-Khomsi, Mohamed Salem, and Suleiman Rahil, who were friendly and helpful companions in the field. Others to whom I am indebted include Bashir Weheshi, Abdul Salem Krayem, Mouktar Ali Ahmed, Araby Mohamed, Ahmed Aboukhader, Jusuf Abu Alahbas, Milad Shalih, I. M. Aly, and also the project director at Wadi al Bab, whom I remember fondly but merely as Mr. Fadel. Professor Moid Ahmad of Ohio University helped to arrange my visit, and Professor Gene Mapes, also of Ohio University, provided me with a preliminary report on *Lecanora* that he had submitted to the Libyan government.

I am especially grateful to Lisa Bush, who provided drawings of the species most commonly referred to as lichen manna. Richard C. Harris of the New York Botanical Garden gave me the benefit of his lichenological insights, and William R. Buck, also at New York, sleuthed out bibliographic references for me.

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THE GYMNOSPERMS OF MOUNT KINABALU

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INTRODUCTION

Mount Kinabalu, in the Malaysian state of Sabah in northern Borneo, is the highest mountain in Borneo and between the Himalayas and New Guinea. It encompasses an area of about 700 km^2, and ranges in elevation from slightly above sea level to a maximum height of 4101 m on Low's Peak. Geologically, Kinabalu is one of the most recent major massifs in the world. It is an adamellite (granitic) pluton, which has been uplifted diapirically in the last 1.5 million years and may still be rising at a rate of about 0.3 cm/year. During the Pleistocene the summit supported an ice cap 5 km^2 in extent. Deglaciation of the summit occurred about 9,200 years ago. Moraines have been observed as low as about 3,000 m (Jacobson 1978; Myers 1978).

Kinabalu is thought to have one of the richest floras in the world for a local area (Beaman & Beaman 1990), with more than 4,000 species of vascular plants. Over 180 families and 950 genera occur in the flora. The high species diversity apparently results from a combination of factors, among which the most important are: 1) great altitudinal and climatic range from tropical rain forests near sea level to freezing alpine conditions at the summit; 2) precipitous topography causing effective geographic and reproductive isolation of species over short distances; 3) geological history of the Malay Archipelago; 4) a diverse geology with many localized edaphic conditions, particularly serpentine or ultramafic substrates; and 5) frequent climatic oscillations influenced by El Niño events.

While preparing a botanical inventory of all vascular plants on Mount Kinabalu, we have accumulated data on the gymnosperms that are ready to publish, hence this report. Accounts of the pteridophytes (Parris et al. 1992) and the orchids (Wood et al. 1993) have already been published. Those studies recognized 620 pteridophyte and 711 orchid taxa. The remaining monocot and dicot families are not yet ready for publication. The Kinabalu gymnosperms have not previously been the subject of an independent publication, notwithstanding that some of them are dominants or subdominants in the high-elevation vegetation. Furthermore, certain species have economic value as timber trees, although their limited occurrence on Kinabalu is mostly protected within Kinabalu Park.

The enumeration that forms the body of this paper includes three families of Coniferales, namely Araucariaceae, Phyllocladaceae, and Podocarpaceae and the Gnetaceae (Gnetales). Nine genera are recognized; the number of species and additional infraspecific taxa are indicated in parentheses as follows. Araucariaceae:

Agathis (3); Phyllocladaceae: *Phyllocladus* (1); Podocarpaceae: *Dacrycarpus* (2); *Dacrydium* (5); *Falcatifolium* (1); *Nageia* (1); *Podocarpus* (6); *Sundacarpus* (1); Gnetaceae: *Gnetum* (6; 2). Thus, 26 species of gymnosperms, and two additional varieties, are currently recognized in the Kinabalu flora. The occurrence of 28 gymnosperm taxa in the limited area of Mount Kinabalu would seem to indicate that they represent a rather diverse component in terms of world-wide gymnosperm diversity, but we lack data for comparable areas.

HISTORICAL ASPECTS

The first account of Kinabalu gymnosperms was by Stapf (1894) in his scholarly treatise, "On the Flora of Mount Kinabalu, in North Borneo." He listed five species, only four of which were fully determined. Two of the species Stapf treated had names in approximate agreement with those in the present account. Twenty years later Stapf (1914) reported seven gymnosperms, based on the materials in his previous study with the addition of the 1910 collections by Lilian S. Gibbs.

Subsequent to the reports by Stapf, Meijer (1965a) mentioned nine taxa, including the genera *Gnetum*, *Phyllocladus*, *Podocarpus*, *Dacrydium*, and *Agathis*. Most of these were also illustrated by him (Meijer 1965b). Corner (1978) listed 13 species of conifers, but one of these (*Podocarpus glaucus*) is not presently considered to occur in Borneo and another (*Podocarpus polystachyus*) is a strictly coastal species. Cockburn (1980), although not attempting to list the gymnosperms of Kinabalu, included 12 species that occur on the mountain and illustrated most of them.

The two most important publications relating to the taxonomy of the gymnosperms of Mount Kinabalu are the *Flora Malesiana* treatments of *Gnetum* (Markgraf 1951) and of the Coniferales (de Laubenfels 1988). The present account follows those treatments in generic and species concepts, but some varieties of *Gnetum* proposed by Markgraf are not recognized. Not all taxonomists would accept the generic concepts of de Laubenfels for segregates of *Podocarpus* and *Dacrydium*, nor his species distinctions in *Agathis*, but during this study they appeared to be useful distinctions that are followed here.

COLLECTIONS OF KINABALU GYMNOSPERMS

Up to 1931 only about 26 specimens of gymnosperm had been collected on the mountain, four by H. Low in 1851 or 1858, five by G. D. Haviland in 1892, 11 by L. S. Gibbs in 1910, and 6 by M. S. Clemens in 1915. In 1931–33 J. and M. S. Clemens collected intensively on the south and west sides of the mountain, probably obtaining over 9000 numbered collections plus many others that they did not number. Our records include 106 of their gymnosperm collections from that period. Other significant collections of gymnosperms have been obtained by the Royal Society expeditions in 1961 (Chew, Corner & Stainton) and 1964 (Chew & Corner) (32 numbers), by W. Meijer (23 numbers) in 1959–1963, by S. Kokawa and M. Hotta (21 numbers) in January–February, 1969, by P. F. Cockburn and Aban Gibot (17 numbers) in 1976, by D. J. de Laubenfels (the only taxonomist specializing in gymnosperms ever to have collected on the mountain; 43 numbers) in August, 1978, and January, 1979, and by the Beaman team (29 numbers) in 1983–84 and 1992. Even now the Kinabalu gymnosperms could hardly be said to be well

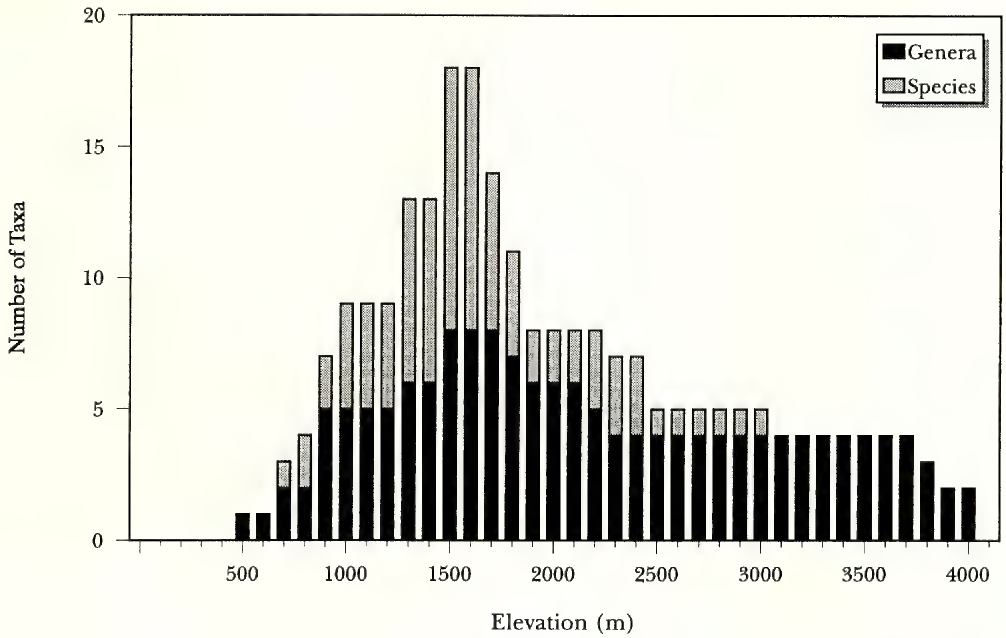

FIG. 1. Elevational distribution of gymnosperms on Mount Kinabalu.

collected; the present study is based on about 446 collections and 700 specimens obtained by 74 collectors or collecting teams.

ECOLOGICAL CONSIDERATIONS

Gymnosperms are scattered in the Kinabalu vegetation from the lowest to highest elevations. They are ecological dominants just below the summit area. Kitayama (1991) recognized 'Tropical lower-subalpine coniferous forest' and 'Tropical upper-subalpine forest'; the dominant species include the gymnosperms *Phyllocladus hypophyllus* and *Dacrycarpus kinabaluensis*, along with the angiosperm trees (or shrubs) *Leptospermum recurvum*, *Eugenia (Syzygium) kinabaluensis*, *Rhododendron buxifolium*, and *Schima brevifolia*. In addition to these two important gymnosperms in the summit flora, Fig. 1 shows that two other species (*Podocarpus brevifolius* and *Dacrydium gibbsiae*) also extend to high elevations.

In spite of the relative importance of gymnosperms in the high-elevation vegetation of Kinabalu, maximum gymnosperm generic and specific diversity occurs at about 1500 m (Fig. 1), a circumstance that also pertains to the pteridophytes (Parris et al. 1992) and orchids (Wood et al. 1993). Corner (1978) noted that *Agathis* was a common big tree from the Mesilau River across the Pinosuk Plateau. Much of that area is at an elevation of about 1500 m. The natural vegetation of the Pinosuk Plateau, formerly part of Kinabalu Park, has been virtually destroyed by various development projects in the past 10 years. Ironically, some spindly pines (*Pinus*) have been planted on the Pinosuk Plateau golf course, probably in almost the exact spot where magnificent *Agathis* trees once stood. *Agathis* was also common in the lower-elevation hill forest on the ultramafic Hempuen Hill, but after that area was degazetted from the Park in 1984, it became a virtual free-for-all for various land grabs, logging, and unsuccessful slash-and-burn agriculture. Most of that forest spared from such activities was consumed by forest fires in 1990.

The species of *Gnetum* are all lianas, often large and extending high into tree crowns in the lowlands, hill forest, and lower montane forest. *Gnetum latifolium* var. *minus* extends up to 1800 m at Tinekuk Falls and *G. leptostachyum* var. *abbreviatum* to the same elevation in the Kilembun basin and at Marai Parai, if Clemens elevation data are to be believed. The rare species *G. gnemonoides* (from the east side of Kinabalu), with huge seeds, and *G. klossii* (from the west side) are known only from lowlands and hill forest, respectively. *Gnetum cuspidatum* and *G. neglectum* are not readily distinguishable from the relatively common *G. leptostachyum* var. *leptostachyum*, which occurs in hill forest and lower montane forest at a number of localities.

Possibly the most abundantly collected of all species in the Kinabalu flora is *Phyllocladus hypophyllus*, now known from 60 collections and 91 specimens. As noted by Corner (1978), it is an Australasian element and extends from Borneo to Sulawesi, Maluku, the Philippines, and New Guinea; other species are known from New Zealand and Tasmania. Keng (1974) considered *Phyllocladus hypophyllus* to be the most primitive living gymnosperm. We have seen large trees of it on the Pinosuk Plateau, but at the highest elevations it is reduced to a low shrub or treelet.

Dacrycarpus imbricatus var. *patulus* and *D. kinabaluensis* are related taxa that were originally treated as the same species; however, they seem readily distinguishable and occur exclusively at different elevations. *Dacrycarpus imbricatus* var. *patulus* is a species of lower montane forest, hardly occurring above 2000 m. *Dacrycarpus kinabaluensis*, on the other hand, is a strictly high-elevation species of upper montane forest and summit scrub, which rarely occurs below 2500 m. De Laubenfels (1988) noted that on Kinabalu *D. imbricatus* does not occur above 2000 m, and indeed the high-elevation figure we have is based on the specimen *Clemens 33618* from the Penataran basin and may be erroneous. *Dacrycarpus imbricatus* is widely distributed in Borneo, Southeast Asia, the Malay Peninsula, Sumatra, Mindanao, Sulawesi, New Guinea, the New Hebrides, and Fiji, whereas *D. kinabaluensis* is endemic to Mount Kinabalu.

One of the most distinctive trees in the upper montane forest is *Dacrydium gibbsiae*, conspicuous along the summit trail from about 2500 m to 3000 m. The species is a very graceful plant of 'Christmas tree' aspect with drooping lower branches. It appears to be restricted to ultramafic substrates, such as those in the area of mossy forest on ridges between Layang-layang and Paka-paka Cave. Found just below this area, in a zone from about 2000 to 2500 m, is *Dacrydium xanthandrum*, readily distinguishable because its leaves are slightly longer than those of *D. gibbsiae*, and extend perpendicular to the stem rather than curving stiffly upward and inward as in *D. gibbsiae*.

Along the road from Park Headquarters to the Power Station, in the elevation range of 1500 to 1800 m, several gymnosperms can be seen, including *Agathis kinabaluensis*, *A. lenticulata*, *Dacrycarpus imbricatus* var. *patulus*, *Dacrydium gracilis*, *Falcatifolium falciforme*, *Podocarpus laubenfelsii,* and *Sundacarpus amara*. In this area Cockburn performed a useful service by collecting lower, middle, and upper branches from trees of several different species. Through these collections one can better understand the extent of foliage variation on individual trees and thus better interpret specimens for which the collector did not indicate the part of the tree from which they were obtained.

Eight of the Kinabalu gymnosperms (i.e., about one-third of the taxa) are found predominantly or entirely on ultramafic substrates. These are: *Agathis borneensis*, *Gnetum leptostachyum* var. *abbreviatum*, *Dacrydium gibbsiae*, *D. pectinatum*, *Podocarpus brevifolius*, *P. confertus*, *P. gibbsii,* and *P. globulus*. Ultramafic

substrates are extremely important in the occurrence of orchids on Kinabalu (Wood et al. 1993), but proportionally fewer of the gymnosperms seem restricted to ultramafic substrates.

The following six taxa are thought to be endemic to Mount Kinabalu: *Agathis kinabaluensis*, *Gnetum leptostachyum* var. *abbreviatum*, *Dacrycarpus kinabaluensis*, *Dacrydium gibbsiae*, *Podocarpus brevifolius*, and *P. gibbsii*. Five others, i.e., *Dacrydium gracilis*, *Podocarpus confertus*, *P. globulus*, *P. laubenfelsii,* and *Agathis lenticulatus,* are endemic to Borneo. The other species are largely centered in the Malesian region, particularly Borneo; *Phyllocladus hypophyllus* is the conspicuous Australasian element.

METHODS

The overall concept of the botanical inventory of Mount Kinabalu as a taxonomic database was outlined by Beaman and Regalado (1989). An integrated system of computer programs used for data editing and printing the gymnosperm enumeration (as well as those for other parts of the project) was written in the dBASE IV programming language by Reed Beaman. A management program, KINABALU, allows for accessing any aspect of the database through a menu system. Six principal relational data files were employed. Two of these files contain data on specimens including types. Taxonomic, nomenclatural, and bibliographic information is linked from other files. Various procedures permit creating and editing a database. Menus facilitate inputting and editing specimen and taxon data, globally replacing various expressions such as changing an author's name or abbreviation, indexing and querying the database, computing a summary of elevation ranges for taxa, numbering taxa, making an index to numbered collections, and printing enumerations of all taxa in the database or selected families or genera.

One objective of the project has been to examine critically all specimens upon which the Enumeration is based. For the gymnosperms, these include approximately 700 specimens located in six herbaria: BM, K, L, MSC, SING, and SNP (Sabah Parks Herbarium on Mount Kinabalu). From an examination of specimen citations it can be seen that certain species have been very much collected on the mountain and others very little. In the case of the rather conspicuous gymnosperms, the number of specimens cited probably is a fairly good indicator of the frequency of that taxon on the mountain.

For purposes of brevity, and especially to facilitate effective queries of the database, we have used standardized locality data in the Enumeration. A list of the standardized locality names, with their geographic coordinates, is provided by Beaman et al. (in press). It may be noted that some locality names are rather different from those on specimens and in the literature, because we have attempted to use spellings established in accordance with the modern Dusun language.

Elevation data are summarized for all taxa for which these data were available on specimen labels. The elevation range indicated for taxa is based on the lowest and highest elevations recorded (whether in feet or meters) for specimens of each taxon and rounded to the nearest 100 m. In some taxa certain specimens have no elevation data while others do. It may be apparent from the locality data that a particular taxon must occur at lower or higher elevations than indicated by the elevation recorded. We have refrained from providing elevation ranges for taxa when the specimens do not provide this information, with the result that the elevations stated are sometimes misleading or incorrect.

Taxonomic treatments that the Enumeration follows are indicated at the beginning of each family and genus. Type specimens are cited only for taxa described from Mount Kinabalu. The synonymy includes only names based on types from Kinabalu. Names of authors of taxa are abbreviated in accordance with the standardized list of author abbreviations (Brummitt & Powell 1992).

In order to produce an index of determined specimens, it is necessary to have the taxa numbered. In the treatment of pteridophytes for the Kinabalu inventory, 30 families were recognized and numbered in alphabetical order. The gymnosperms start with family 31 and likewise are numbered in alphabetical order, except that the Gnetaceae are placed after the conifers as family 34. Therefore, the numbering of the gymnosperms begins with the Araucariaceae as family 31 and goes on to the other families. Within each family the genera are alphabetically numbered and likewise species within genera. Nominate subspecies or varieties always precede other infraspecific taxa, regardless of alphabetical order.

TAXONOMIC PROBLEMS

The enumeration of *Gnetum* presented here may not be very sound. Markgraf's treatment in *Flora Malesiana* was based largely on his earlier (1930) monograph. At the time of that work hardly any specimens of *Gnetum* from Kinabalu had been collected. Relatively few of the specimens we examined have his annotations. *Gnetum* is particularly difficult because some of the best characters are in the seeds and the branches on which they are borne. Since the plants are dioecious, a rather high percentage of specimens lack these reproductive structures. The characters of leaf venation that Markgraf used also are difficult to recognize and probably do not hold up very well. A modern taxonomic account of the genus is much needed.

Agathis is also a difficult genus, and the two higher-elevation species recognized in this account (*A. kinabaluensis*, *A. lenticulata*) may be local ecological variants. On Kinabalu, however, they seem reasonably distinguishable and are therefore retained. An alternative view of *Agathis* is provided by Whitmore (1980), who included material here recognized in *A. kinabaluensis* and in *A. lenticulata* as *A. dammara* (Lamb.) Rich. subsp. *dammara*. According to Whitmore's treatment, *A. dammara* does not occur in Borneo except in some mountainous areas. Whitmore emphasized characters of the male cones and considered leaf shape and size to be highly and continuously variable.

Cockburn (1980) indicated that the splitting of *Podocarpus* into several smaller genera was difficult to condone when even the differences between *Dacrydium* and *Podocarpus* are so fine as to make these genera unworthy of separation. He regarded *Podocarpus imbricatus* (i.e., *Dacrycarpus imbricatus*) as a large, widespread species with a number of ecotypes associated with altitude and exposure in which the proposed varieties merge imperceptibly into one another. We find, however, that *Dacrycarpus kinabaluensis* and *D. imbricatus* are almost always readily distinguishable. Page (1988) noted that the diagnoses of many of these genera often depend heavily on vegetative aspects of the plants, in a group whose reproductive aspects offer a rather limited array of features. He further indicated that most of the small genera in the Podocarpaceae are fairly natural groupings with good geographic and probably evolutionary cohesion, supported in many cases by cytological and phytochemical data.

Because of the utility of vegetative characters in distinguishing many of the taxa, we have included a vegetative key to genera and have provided figures for all the taxa, which mostly represent vegetative characters. We hope the emphasis of such features will facilitate identification, because many specimens are collected in sterile condition.

A few specimens of *Podocarpus* are tentatively determined. One of these is *Beaman 10362* from Mamut Copper Mine. This collection lacks the distinctively erect disposition of the leaves, characteristic of *Podocarpus brevifolius*, and occurs at a lower elevation than normal for the species. However, it seems to be more in accord with that taxon than any other currently recognized species.

The juvenile material, or perhaps lower branches, that collectors have obtained of certain species sometimes makes identification difficult. For example, in the mature state and from upper branches, *Dacrydium gibbsiae* and *D. gracilis* are highly distinctive, but young individuals or lower branches can have a different aspect with much longer and more similar leaves.

VEGETATIVE KEY TO THE GENERA OF GYMNOSPERMS ON MOUNT KINABALU

1. Large woody climbers. Leaves opposite, of dicotyledonous aspect. *Gnetum.*
1. Trees, or, at high elevations, shrubs. Leaves or phyllodes opposite or alternate, more or less scleromorphic.
   2. True leaves absent, these replaced by cladodes or flattened shoots. *Phyllocladus.*
   2. Leaves present, needlelike, scalelike, or expanded into broad blades.
      3. Leaves opposite, the largest more than 2 cm wide.
         4. Terminal buds globose. *Agathis.*
         4. Terminal buds acute. *Nageia.*
      3. Leaves spirally arranged, less than 2 cm wide.
         5. Leaves, at least some of them, more than 3 cm long.
            6. Principal leaves bilaterally flattened, falcate. *Falcatifolium.*
            6. Principal leaves with distinct upper and lower surface.
               7. Midvein on the upper surface with a longitudinal groove. *Sundacarpus.*
               7. Midvein not grooved. *Podocarpus.*
         5. Leaves all relatively small, needlelike or scalelike, less than 3 cm long.
            8. Foliage dimorphic. *Dacrycarpus.*
            8. Foliage not dimorphic, needlelike. *Dacrydium.*

ENUMERATION OF TAXA

Kramer, K. U., & Green, P. S., eds. The Families and Genera of Vascular Plants. Kubitzki, K., ed. I. Pteridophytes and Gymnosperms. Springer-Verlag, Berlin etc.; Gymnosperms, pp. 279–391. 1990.

31. Araucariaceae

De Laubenfels, D. J. Araucariaceae. Fl. Males. I, 10: 419–442. 1988.

31.1. Agathis

De Laubenfels, D. J. *Agathis*. Fl. Males. I, 10: 429–442. 1988. De Laubenfels, D. J. The species of *Agathis* (Araucariaceae) of Borneo. Blumea 25: 531–541. 1979.

31.1.1. Agathis borneensis Warb., Monsunia 1: 184. 1900. Fig. 2.

Large tree. Hill forest, sometimes on ultramafic substrate. Elevation: 800–1400 m.

Specimens Examined. Dallas: 900 m, *Clemens 27302* (BM); Hempuen Hill: 800–1000 m, *Beaman 7425* (MSC), 800–1200 m, *7694* (K, MSC), 1400 m, *Beaman et al. SNP 5068* (SNP); Mt. Nungkek: 900–1200 m, *Clemens 32821* (BM, L).

31.1.2. Agathis kinabaluensis de Laub., Blumea 25: 535. 1979.—Type: Summit Trail, 2000 m, *de Laubenfels P 625* (holotype: L!). Fig. 3.

Small to large tree. Lower montane forest, sometimes in mossy forest on ridges. Elevation: 1500–2200 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Bambangan River: 1500 m, *RSNB 4457* (K, SING); Eastern Shoulder: *Phillipps SNP 2165* (SNP); Kiau: *Clemens 10004* (BM, K); Kiau View Trail: 1600 m, *Beaman et al. SNP 5077* (SNP), 1600 m, *Justine SNP 675* (SNP), 1600 m, *SNP 767* (SNP); Kilembun Basin: 1700 m, *Clemens 34496* (BM, K, L); Mempening Trail: 1700 m, *de Laubenfels P 646* (L); Mesilau Cave: 1900–2200 m, *Beaman 9556* (K, MSC), 1800 m, *RSNB 4778* (K, SING); Mt. Tembuyuken: *Nais et al. SNP 4826* (SNP); Park Headquarters: 1700 m, *Gimpiton et al. SNP 937* (SNP), 1700 m, *de Laubenfels P 644* (L), 1700 m, *P 720* (L).

31.1.3. Agathis lenticulata de Laub., Blumea 25: 537. 1979.—Type: Park Headquarters, 1500 m, *de Laubenfels P 619* (holotype: L!). Fig. 4.

Large tree. Lower montane forest. Elevation: 900–1800 m.

Additional Specimens Examined. Kilembun Basin: 1700 m, *Clemens 34496* (BM); Liwagu River Trail: 1500 m, *Lajangah SAN 44400* (K, L), 1500 m, *Sadau SAN 42812* (K, L), 1500 m, *de Laubenfels P 637* (L); Mamut Hill: 1500–1800 m, *Kokawa & Hotta 5676* (L); Mesilau River: 1500 m, *RSNB 4249* (K, L, SING), 1500 m, *RSNB 4330* (K, L, SING), 1500 m, *de Laubenfels P 621* (L); Mesilau/Bambangan Rivers: 1600–1700 m, *Kokawa & Hotta 4280* (L); Mount Kinabalu: *Aban SAN 56636* (SNP), 1700 m, *Binideh SAN 65171* (SING), 1600 m, *Dolois & Ansow SNP 1941* (SNP); Park Headquarters: 1400 m, *Abbe et al. 9973* (L), 1600 m, *Beaman & Ansow SNP 5060* (SNP), 1600 m, *Binideh SAN 65143* (K), *SAN 65144* (SNP), 1600 m, *Kokawa & Hotta 6128* (L), 1500 m, *Lowry 649* (L), 1200 m, *Meijer SAN 22111* (K), 1600 m, *Phillipps SNP 1516* (SNP), 1500 m, *de Laubenfels P 620* (L); Penibukan: 1200 m, *Clemens 40732* (BM); Tenompok: 1500 m, *Clemens 28145* (BM), 1500 m, *28390* (BM, K, L), 1500 m, *28729* (BM, K), 1400 m, *Melegrito A 473* (K, L, SING), 1400 m, *Smythies S 10602* (K, L, SING); Tenompok/Ranau: 1500 m, *Carr SFN 27005* (SING).

32. Phyllocladaceae

32.1. Phyllocladus

De Laubenfels, D. J. *Phyllocladus*. Fl. Males. I, 10: 355–360. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 277–282. 1969. Keng, H. 1978. The genus *Phyllocladus* (Phyllocladaceae). J. Arnold Arb. 59: 249–273.

32.1.1. Phyllocladus hypophyllus Hook. f., Icon. Pl. n.s. 5: t. 889. 1852.—Type: Mount Kinabalu, 2400 m, *Low s.n.* (holotype: K!). Fig. 5.

Large to small tree, shrubby and gnarled at high elevations. Lower montane forest, upper montane forest, mossy forest on ridges, low mossy and xerophyllous scrub. Elevation: 1200–4000 m.

Additional Specimens Examined. Eastern Shoulder: 2300 m, *RSNB 710* (K, L, SING); Gurulau Spur: 2400–2700 m, *Clemens 50626* (BM), *50784* (BM, L), 3000 m, *50797* (BM, L), 3400–3700 m, *51220* (BM); Kemburongoh: 2100 m, *Mikil SAN 56277* (K, L), 2100 m, *Price 183* (K), 2100 m, *Sinclair et al. 9053* (SING), 2200 m, *Smith 453* (L); Kinateki River Head: 2100 m, *Clemens 31838* (L); Kundasang: *Burgess SAN 25167* (K), 1500–1800 m, *Meijer SAN 21968* (K); Layang-layang: 2200 m, *Andrews 883* (K); Lubang: 1800 m, *Gibbs 4152* (BM, K); Mamut Copper Mine: *Aban SAN 66823* (SING); Marai Parai: 1500 m, *Clemens 31927* (K), 1500 m, *32459* (BM, L); Marai Parai Spur: *Clemens 10957* (BM), 2100 m, *Gibbs 4088* (BM, K); Mesilau Basin: 2400–2700 m, *Clemens 29743* (BM, K, L); Mesilau Cave: 1800 m, *RSNB 4824* (K, SING); Mesilau Cave Trail: 1700–1900 m, *Beaman 8000* (MSC); Mesilau River: 1500 m, *RSNB 4172* (K, L, SING); Mesilau Trail: *Chow & Leopold SAN 74513* (K, L); Minetuhan Spur: 1800–2100 m, *Clemens 33864* (BM); Mount Kinabalu: 3400 m, *Haviland 1092* (BM, K, L, SING), 3000 m, *Low s.n.* (K), 3400 m, *Native Collector 39* (K), 2700 m, *Nicholson SAN 17823* (K, SING), *Rao et al. 76* (SING), 3100 m, *Rickards 161* (K); Mt. Tembuyuken: *Nais et al. SNP 4830* (SNP); Paka-paka Cave: 3100 m, *Carr SFN 27632* (SING), *Clemens 10565* (K), 3400 m, *27930* (BM, L), 3000 m, *29328* (BM, K, L, SING), 3200 m, *30030* (K), 3000 m, *Gibbs 4238* (BM), 3100 m, *Holttum s.n.* (SING), 3000 m, *Meijer SAN 29271* (K, L), 2700 m, *Smythies S 10622* (K, L, SING), *Wyatt-Smith 80371* (K, L, SING); Paka-paka Cave/Panar Laban: 3200–3400 m, *Kokawa & Hotta 3451* (L), 3200–3400 m, *3497* (L); Paka-paka Cave/Summit Area: 2700–3700 m, *Gibbs 4273* (BM, K); Panar Laban: 3500 m, *Beaman 8297* (MSC), 3400 m, *Nais & Dolois SNP 3277* (SNP), 3300 m, *Smith 474* (L), 3400 m, *Stone 11348* (L), 3400 m, *11373* (L); Park Headquarters: 1200 m, *Meijer SAN 22114* (K), 1700 m, *de Laubenfels P 645* (L); Park Headquarters/Power Station: 1600 m, *Cockburn & Aban SAN 82973* (K, L); Pig Hill: 2000–2300 m, *Beaman 9843* (MSC); Sayat-sayat: 3500 m, *Carr SFN 27617* (BM, SING); Sheila's Plateau: 3400 m, *Fuchs & Collenette 21430* (K); Summit Area: 3600 m, *Anderson S 27089* (K), 3600 m, *S 27090* (L), 3400–4000 m, *Kokawa & Hotta 3563* (L); Summit Trail: 3100 m, *de Laubenfels P 636* (L).

33. Podocarpaceae

De Laubenfels, D. J. Podocarpaceae. Fl. Males. I, 10: 351–419. 1988.

33.1. Dacrycarpus

De Laubenfels, D. J. *Dacrycarpus*. Fl. Males. I, 10: 374–384. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 315–337. 1969.

33.1.1. Dacrycarpus imbricatus (Blume) de Laub.

33.1.1a. Dacrycarpus imbricatus var. **patulus** de Laub., J. Arnold Arb. 50: 320. 1969. Fig. 6.

Large tree. Lower montane forest. Elevation: 1400–2400 m.

Specimens Examined. Gurulau Spur: 1700 m, *Clemens 50696* (BM), 2300 m, *51024* (BM); Kadamaian River: 2000 m, *Carr SFN 27735* (SING); Kemburongoh: 2000 m, *Carr SFN 27553* (BM, SING), 1500 m, *Clemens 28954* (K), 1500 m, *Fosberg 44128* (K, L); Kiau View Trail: *Aban SAN 56305* (SING); Kinateki River Head: 2400 m, *Clemens 35011* (BM); Kundasang: *Burgess SAN 25162* (SING); Liwagu River Trail: 1500 m, *Sadau SAN 42811* (SNP); Mamut Hill: 1400–1700 m, *Kokawa & Hotta 5384* (L); Mamut/Bambangan River: 1400–1700 m, *Kokawa & Hotta 5514* (L); Mesilau Cave Trail: 1700–1900 m, *Beaman 8008* (MSC); Mesilau River: 1500 m, *RSNB 4084* (K, L, SING), *Clemens 51635* (BM, K, L); Mount Kinabalu: *Lajangah SAN 33085* (K, L, SING); Park Headquarters: *Abbe et al. 9994* (SING), *Tan & Gimpiton SNP 507* (SNP), 1600 m, *Thomas & Patrick SNP 235* (SNP); Park Headquarters/Power Station: 1600 m, *Cockburn & Aban SAN 82961* (K, L), 1700–1900 m, *Kokawa & Hotta 3217* (L), 1600 m, *Mikil SAN 33930* (SNP); Penataran Basin: 2400 m, *Clemens 33618* (BM, K, L); Pinosuk Plateau: *Chow & Leopold SAN 74521* (K, L, SING), 1500 m, *Sadau SAN 42890* (K, L); Sosopodon: 1500 m, *Sario SAN 32246* (K); Tenompok: 1500 m, *Clemens 28631* (BM, K, L, SING), 1500 m, *29779* (BM, K, L), 1400 m, *Melegrito A 471* (K, L, SING), 1400 m, *Smythies S 10601* (K, L, SING); Tenompok/Ranau: 1500 m, *Carr SFN 27010* (SING).

33.1.2. Dacrycarpus kinabaluensis (Wasscher) de Laub., J. Arnold Arb. 50: 330. 1969. Fig. 7.

Podocarpus cupressina Stapf, non R. Br. ex Mirbel, Trans. Linn. Soc. Bot. 4: 249. 1894.

Podocarpus imbricatus Blume var. *kinabaluensis* Wasscher, Blumea 4: 400. 1941.—TYPE: Above Paka-paka Cave, 3900 m, *Clemens 27854* (holotype: B†; isotype: BM!).

Shrub, treelet, or small tree, frequently gnarled. Upper montane forest, especially on ultramafic substrate, extending to upper limit of scrub vegetation. Elevation: 2100–4000 m. Endemic to Mount Kinabalu.

ADDITIONAL SPECIMENS EXAMINED. EASTERN SHOULDER: 3200 m, *RSNB 868* (K, L, SING), *Phillipps et al. SNP 2388* (SNP); GURULAU SPUR: 3000 m, *Clemens 51066* (BM), 3400 m, *51201* (BM, L); JANET'S HALT: 2400 m, *Collenette 579* (K); LAYANG-LAYANG/PANAR LABAN: 2700–3400 m, *Kokawa & Hotta 3380* (L); LUBANG/GRANITE CAP: *Gibbs 4216* (K); MARAI PARAI: 3000–3400 m, *Clemens 32316* (K, L), 3000–3400 m, *32316A* (BM), 3400 m, *32317* (BM, L), 3400 m, *32318* (BM, L); MARAI PARAI SPUR: *Gibbs 4216* (BM); MESILAU FRONT: 2700–3400 m, *RSNB 5887* (K, L); MOUNT KINABALU: *Binideh SAN 65173* (K), 3100 m, *Cockburn SAN 82988* (K), 3200 m, *Cockburn & Aban SAN 82972* (K), 3200 m, *SAN 82978* (K, L), 3200 m, *SAN 82981* (K), 3400 m, *Haviland 1094* (K, SING), 3400 m, *1095* (K, SING), 3000 m, *Nicholson SAN 17825* (K, SING), 2700 m, *SAN 39766* (K, L, SING), 2100 m, *Rao et al. 83* (SING); PAKA-PAKA CAVE: 3100 m, *Carr SFN 28052* (SING), 3400 m, *Clemens 28910* (K, L), 3100 m, *Holttum s.n.* (SING), 3000 m, *Meijer SAN 21988* (K), 3000 m, *SAN 29265* (K, L), 3300 m, *Sinclair et al. 9146* (K, SING), 3200 m, *Wood & Wyatt-Smith SAN 4493* (SING); PAKA-PAKA CAVE/PANAR LABAN: 3200 m, *Wood & Wyatt-Smith SAN 4493* (L); PANAR LABAN: 3500 m, *Anonymous SNP 2337* (SNP), 3400 m, *Boeriaatmadja 89* (L), *Justine SNP 676* (SNP), 3400 m, *Phillipps & Tan SNP 1594* (SNP), 3300 m, *Smith 471* (L), 3400 m, *Stone 11368* (L); PANAR LABAN/SAYAT-SAYAT: 3400–3700 m, *Sato UKMS 764* (SNP); SAYAT-SAYAT: 3800 m, *Cockburn & Aban SAN 82771* (K, L); SUMMIT AREA: 3400 m, *Anderson S 27079* (K), 4000 m, *Clemens 27092* (BM, K, L), 3800 m, *29914* (K, L), 3700 m, *Kokawa & Hotta 3640* (L), 3600 m, *3642* (L); SUMMIT TRAIL: 2800–3000 m, *Beaman SNP 5062* (SNP), 3000 m, *8305* (K, MSC), *Clemens 10636* (K), 3600 m, *Jacobs 5755* (K, L), 2800 m, *de Laubenfels P 631* (L), 2800 m, *P 632* (L), 3100 m, *P 635* (L).

33.2. Dacrydium

De Laubenfels, D. J. *Dacrydium*. Fl. Males. I, 10: 360–371. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 282–308. 1969.

33.2.1. Dacrydium beccarii Parl. in DC., Prodr. 16, 2: 494. 1868. Fig. 8.

Shrub or small tree. Lower montane forest, probably on ultramafic substrate. Elevation: 1500–1600 m. This record may be questionable, but the specimen cited was determined by de Laubenfels.

SPECIMEN EXAMINED. MAMUT HILL: 1500–1600 m, *Kokawa & Hotta 6051* (L).

33.2.2. Dacrydium gibbsiae Stapf in Gibbs, J. Linn. Soc. Bot. 42: 192. 1914.—TYPE: Lubang/Granite Core, 1800–3700 m, *Gibbs 4162* (holotype: BM!; isotype K!). Fig. 9.

Dacrydium beccarii Parl. in DC. var. *kinabaluense* Corner, Gardens' Bull. 10: 244, t. 9. 1939.—TYPE: Penibukan, 1400 m, *Carr SFN 26437* (holotype: SING!).

Shrub or small tree with pendulous branches. Upper montane forest on ridges, rarely lower montane forest, often on ultramafic substrate. Elevation: 1400–3700 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Kemburongoh/Paka-paka Cave: 2700–3400 m, *Clemens s.n.* (BM); Layang-layang: 2700–2900 m, *Hotta 3897* (L), 2700–2900 m, *3900* (L); Layang-layang/Paka-paka Cave: 2700–3200 m, *Kokawa & Hotta 3401* (L); Lubang/Paka-paka Cave: *Clemens 10685* (BM, K); Marai Parai: 1600 m, *Argent SNP 2379* (SNP), 1600 m, *Carr SFN 26588* (SING), 1500–1800 m, *Clemens 33037* (BM, L), 1500 m, *Collenette A 100* (BM); Marai Parai Spur: 1500–2400 m, *Gibbs 4050* (BM), 1800 m, *Phillipps SNP 1821* (SNP); Mount Kinabalu: 2400 m, *Low s.n.* (K), 2600 m, *Meijer SAN 22045* (K, SING), 2700 m, *Nicholson SAN 17826* (L, SING), 2900–3300 m, *Rickards 153* (K), 2400 m, *Whitehead s.n.* (BM); Paka-paka Cave: 2100–2700 m, *Enriquez SFN 18168* (SING); Penataran Basin: 2000 m, *Clemens 40151* (BM); Penibukan: 1500 m, *Clemens 30922* (BM, L); Pig Hill: 2100 m, *RSNB 4361* (K, L, SING); Pinosuk Plateau: 1600 m, *Collenette 542* (K); Summit Trail: 2800–3000 m, *Beaman SNP 5063* (SNP), 3000 m, *8306* (K, MSC), 2800 m, *de Laubenfels P 628* (L), 2800 m, *P 629* (L), 2200 m, *P 630* (L).

33.2.3. Dacrydium gracilis de Laub., Fl. Males. I, 10(3): 367. 1988.—Type: Park Headquarters, 1500 m, *de Laubenfels P 716* (holotype: L!). Fig. 10.

Large tree. Lower montane forest. Elevation: 1400–1600 m.

Additional Specimens Examined. Hempuen Hill: 1400 m, *Beaman et al. SNP 5070* (SNP); Leteng Trail: 1500 m, *Meijer SAN 21086* (K, SING), 1500 m, *SAN 21098* (K, SING), 1500 m, *SAN 21100* (K, SING); Liwagu River Trail: 1500 m, *de Laubenfels P 638* (L), 1500 m, *P 642* (L); Mesilau River: 1500 m, *RSNB 4303* (K, SING), 1500 m, *RSNB 4305* (K, SING); Park Headquarters: 1500 m, *de Laubenfels P 717* (L); Park Headquarters/Power Station: 1600 m, *Cockburn SAN 82963* (K), 1600 m, *SAN 82965* (K), 1600 m, *Cockburn & Aban SAN 82959* (K), 1600 m, *SAN 82962* (K); Tenompok: 1600 m, *Mujin SAN 33774* (K, L).

33.2.4. Dacrydium pectinatum de Laub., J. Arnold Arb. 50: 289. 1969. Fig. 11.

Medium-sized tree (on Mount Kinabalu). Hill forest on ultramafic substrate. Elevation: 800–1600 m.

Specimens Examined. Hempuen Hill: 800 m, *Abbe et al. 9938* (L), 800 m, *9939* (SING), 1100 m, *9952* (L), 1400 m, *Beaman et al. SNP 5071* (SNP), 900–1200 m, *Meijer SAN 20951* (L), 1200 m, *SAN 20952* (L), 1300 m, *SAN 20970* (K, SING); Kiau View Trail: 1600 m, *Justine SNP 290* (SNP).

33.2.5. Dacrydium xanthandrum Pilger, Bot. Jahrb. 69: 252. 1938. Fig. 12.

Small to medium-sized tree. Lower montane forest, upper montane forest, especially in mossy forest on ridges. Elevation: 1400–3000 m.

Specimens Examined. Janet's Halt: 2400 m, *Collenette 543* (K), 2400 m, *Nicholson SAN 39768* (K); Kemburongoh: 2100 m, *Anonymous SAN 62031* (K), 2100 m, *Meijer SAN 29153* (K, L), 2100 m, *Price 205* (K), 1800 m, *Smythies S 10607* (K, SING); Kilembun River Head: 1800 m, *Clemens 32502* (BM, K, L); Kundasang: 1800 m, *Meijer SAN 23500* (K, SING); Leteng Trail: 1700 m, *Meijer SAN 21097* (K, SING); Mamut/Bambangan Rivers: 1400–1700 m, *Kokawa & Hotta 5565* (L); Mesilau Hill: 2300 m, *RSNB 8024* (K, L); Mount Kinabalu: 1800–2100 m, *Enriquez 18169* (SING), 2000 m, *Haviland 1183* (K, SING), 2700 m, *Holttum s.n.* (SING), 2700 m, *Nicholson SAN 17827* (K, SING); Muru-tura Ridge: 1500–1800 m, *Clemens 34341* (BM, K, L); Paka-paka Cave: 2400–3000 m, *Clemens 28542* (BM); Summit Trail: 2100 m, *Aban SAN 62031* (L), 2100–2300 m, *Beaman & Beaman SNP 5061* (SNP), 2700 m, *Carr SFN 27599* (SING), 2000 m, *Cockburn & Aban SAN 82971* (K), 1800 m, *Smythies S 10607* (L), 2700 m, *de Laubenfels P 626* (L), 2700 m, *P 627* (L).

33.3. Falcatifolium

De Laubenfels, D. J. *Falcatifolium*. Fl. Males. I, 10: 371–374. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 308–314. 1969.

33.3.1. Falcatifolium falciforme (Parl.) de Laub., J. Arnold Arb. 50: 309. 1969. Fig. 13.

Podocarpus falciformis Parl. in DC., Prodr. 16, 2: 685. 1868.
Dacrydium falciforme (Parl.) Pilger, Pflanzenr. IV, 5, Heft 18: 45. 1903.

Small to medium-sized tree. Hill forest, lower montane forest, sometimes on ultramafic substrate. Elevation: 800–2100 m.

Specimens Examined. Hempuen Hill: *Abbe et al. 9940* (SING), 800–1200 m, *Beaman 7668* (MSC), 1400 m, *Beaman et al. SNP 5075* (SNP), 1300 m, *Madani SAN 89369* (K), 1200–1400 m, *Meijer SAN 20279* (L, SING), 1200 m, *SAN 20953* (K), 1500 m, *de Laubenfels P 707* (L); Kemburongoh: 2100 m, *Clemens 27851* (BM, K); Liwagu River Trail: 1500 m, *de Laubenfels P 639* (L), 1500 m, *P 640* (L); Lumu-lumu: 1600 m, *Carr SFN 27241* (SING); Marai Parai: *Argent & Phillipps SNP 2732* (SNP), 1500 m, *Clemens 33078* (K, L), 1500 m, *Holttum s.n.* (SING), *Phillipps SNP 1145* (SNP), *SNP 2762* (SNP); Marai Parai Spur: *Clemens 10962* (K), 1500 m, *Holttum s.n.* (SING); Marai Parai Spur/Dapatan & Penibukan Ridges: 1500 m, *Gibbs 4067* (K); Mesilau River: 1500 m, *RSNB 4847* (K, L, SING); Park Headquarters: 1600 m, *Patrick & Gimpiton SNP 499* (SNP), 1600 m, *Tan & Gimpiton SNP 568* (SNP), 1500 m, *de Laubenfels P 718* (L), 1500 m, *P 719* (L); Park Headquarters/Power Station: 1600 m, *Cockburn SAN 82966* (K, L), 1700–1900 m, *Kokawa & Hotta 3213* (L); Penibukan: 1200–1500 m, *Clemens s.n.* (BM, K, L); Pinosuk Plateau: 1700 m, *RSNB 1863* (K, L, SING).

33.4. Nageia

De Laubenfels, D. J. *Nageia*. Fl. Males. I, 10: 389–395. 1988. De Laubenfels, D. J. Revision of the genus *Nageia* (Podocarpaceae). Blumea 32: 209–211. 1987. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part [*Nageia* as *Decussocarpus*]. J. Arnold Arb. 50: 340–359. 1969. Fu, D. Z. 1992. Nageiaceae—a new gymnosperm family. Acta Phytotax. Sin. 30: 515–528.

33.4.1. Nageia wallichiana (Presl) Kuntze, Rev. Gen. Pl. 2: 800. 1891. Fig. 14.

Medium-sized to large tree. Lower montane forest. Elevation: 1500 m.

Specimens Examined. Mesilau River: 1500 m, *RSNB 4878* (K, L, SING), 1500 m, *de Laubenfels P 624* (L); Penibukan: *Clemens s.n.* (BM); Sosopodon: *Aban SAN 62022* (K, SING).

33.5. Podocarpus

De Laubenfels, D. J. *Podocarpus*. Fl. Males. I, 10: 395–419. 1988. De Laubenfels, D. J. A taxonomic revision of the genus *Podocarpus*. Blumea 30: 251–278. 1985. Wasscher, J. The genus *Podocarpus* in the Netherlands Indies. Blumea 4: 359–542. 1941. Gray, N. E. A taxonomic revision of *Podocarpus*, XI. The South Pacific species of section *Podocarpus*, subsection B. J. Arnold Arb. 39: 424–477. 1958.

33.5.1. Podocarpus brevifolius (Stapf) Foxw., Philipp. J. Sci., Bot. 6: 160, t. 29. 1911. Fig. 15.

Podocarpus neriifolius D. Don in Lambert var. *brevifolius* Stapf, Trans. Linn. Soc. Bot. 4: 249. 1894.—TYPE: Mount Kinabalu, 3400 m, *Haviland 1093* (syntype: K!), 3700 m, *Low s.n.* (syntype: K!).

Small tree or shrub, often gnarled. Mostly upper montane forest, rarely lower montane forest, on ultramafic substrate or in granitic crevices. Elevation: 1200–3800 m. Endemic to Mount Kinabalu.

ADDITIONAL SPECIMENS EXAMINED. EASTERN SHOULDER: 3000 m, *RSNB 724* (K, L, SING), 3000 m, *RSNB 756* (K, L, SING), 2400 m, *Collenette 810* (K, L, SING); GURULAU SPUR: 2100–2700 m, *Clemens 50790* (BM), 3400–3700 m, *50825* (BM, L); LAYANG-LAYANG/PAKA-PAKA CAVE: 2700–3200 m, *Kokawa & Hotta 3411* (L); LAYANG-LAYANG/PANAR LABAN: 2700–3400 m, *Kokawa & Hotta 3379* (L); LUBANG/GRANITE CORE: 1800–3700 m, *Gibbs 4166* (BM); MAMUT COPPER MINE: 1400–1500 m, *Beaman 10362* (K, MSC); MARAI PARAI SPUR: 1500–2400 m, *Gibbs 4089* (BM, K); MESILAU RIVER: 3500 m, *Smith 529* (L); MOUNT KINABALU: 2700–3000 m, *Meijer SAN 22065* (K, SING), 3000 m, *Nicholson SAN 17824* (K, SING), 3400 m, *Rao et al. 77* (SING); MT. TEMBUYUKEN: *Nais et al. SNP 4834* (SNP); PAKA-PAKA CAVE: 3400 m, *Clemens 27103* (BM), 3400 m, *28901* (K, L), 3100 m, *Holttum s.n.* (SING), 3400 m, *Lampangi SAN 29290* (K, L, SING); PANAR LABAN: 3500 m, *Anonymous SNP 2335* (SNP), *Cockburn SAN 82780* (K, L), 3400 m, *Cockburn & Aban SAN 82276* (K), 3400 m, *SAN 82776* (L), 3400 m, *Phillipps & Tan SNP 1586* (SNP), 3400 m, *Stone 11351* (L), 3400–3700 m, *Wong 21* (SING); PENIBUKAN: 1200 m, *Clemens s.n.* (BM, K); SUMMIT AREA: 3400 m, *Anderson S 27094* (K), 3800 m, *Clemens 27826* (BM); SUMMIT TRAIL: 2800–3000 m, *Beaman SNP 5064* (SNP), *Clemens 10657* (K), 3600 m, *Lee et al. SAN 69959* (SNP), 2700 m, *Meijer SAN 21975* (K), 3000 m, *de Laubenfels P 633* (L), 3100 m, *P 634* (L); UPPER KINABALU: 3800 m, *Clemens 27825* (K, L).

33.5.2. Podocarpus confertus de Laub., Blumea 30: 271. 1985. Fig. 16.

Small to large tree. Hill forest on ultramafic substrate. Elevation: 600–1200 m.

SPECIMENS EXAMINED. HEMPUEN HILL: *Aban SAN 90606* (K, L), 600 m, *Madani SAN 89400* (K, L), 1200 m, *de Laubenfels P 712* (L), 1200 m, *P 713* (L), 1200 m, *P 714* (L).

33.5.3. Podocarpus gibbsii N. E. Gray, J. Arnold Arb. 39: 429. 1958.—TYPE: Marai Parai, 1500 m, *Clemens 32021* (holotype: A, n.v.; isotypes BM! K! L!). Fig. 17.

Small to medium-sized tree. Lower montane forest, upper montane forest, mossy ridge forest, on ultramafic substrate. Elevation: 1200–2400 m. Endemic to Mount Kinabalu.

ADDITIONAL SPECIMENS EXAMINED. HEMPUEN HILL: 1500 m, *de Laubenfels P 709* (L), 1500 m, *P 710* (L), 1500 m, *P 711* (L); KILEMBUN BASIN: 1500 m, *Clemens 40001* (BM, K, L); MARAI PARAI: *Phillipps SNP 2761* (SNP); MARAI PARAI SPUR/PENIBUKAN: 1500–2400 m, *Gibbs 4092* (BM, K); PENIBUKAN: 1400 m, *Carr SFN 26450* (SING), 1200–1500 m, *Clemens s.n.* (L); PIG HILL: 2100 m, *RSNB 4369* (K, L, SING).

33.5.4. Podocarpus globulus de Laub., Blumea 30: 269. 1985. Fig. 18.

Small to medium-sized tree. Lower montane forest on ultramafic substrate. Elevation: 1500 m.

SPECIMENS EXAMINED. HEMPUEN HILL: 1500 m, *de Laubenfels P 704* (L), 1500 m, *P 705* (L), 1500 m, *P 706* (L).

33.5.5. Podocarpus laubenfelsii Tiong, Blumea 29: 523. 1984.—TYPE: Park Headquarters, 1500 m, *de Laubenfels P 715* (holotype: L!). Fig. 19.

Small to medium-sized tree. Lower montane forest. Elevation: 1400–1600 m.

ADDITIONAL SPECIMENS EXAMINED. LIWAGU/MESILAU RIVERS: 1400 m, *RSNB 2657* (K, L, SING); MESILAU RIVER: 1500 m, *RSNB 4350* (K, L, SING); PARK HEADQUARTERS: 1600 m, *Aban SAN 49409* (K), 1500 m, *de Laubenfels P 643* (L); SOSOPODON: 1500 m, *Gintus SAN 56374* (K, L).

33.5.6. Podocarpus neriifolius D. Don in Lambert, Gen. Pinus ed. 1: 21. 1824. Fig. 20.

Medium-sized to large tree. Lower montane forest. Elevation: 1100–1700 m.

SPECIMENS EXAMINED. GURULAU SPUR: 1700 m, *Clemens 50691* (BM, K, L); HEMPUEN HILL: 1400 m, *Beaman et al. SNP 5069* (SNP); MESILAU RIVER: 1500 m, *RSNB 4255* (K, L, SING); PENIBUKAN: 1100 m, *Clemens 50051* (BM, K, L).

33.6. Sundacarpus.

De Laubenfels, D. F. *Prumnopitys*. Fl. Males. I, 10: 384–389. 1988.

33.6.1. Sundacarpus amara (Blume) C. N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 378. 1988. Fig. 21.
Prumnopitys amara (Blume) de Laub., Blumea 24: 190. 1978.

Large tree. Lower montane forest. Elevation: 1400–1700 m.

SPECIMENS EXAMINED. KINASARABAN HILL: 1400 m, *Badak SAN 32333* (L); MAMUT/BAMBANGAN RIVERS: 1400–1700 m, *Kokawa & Hotta 5541* (L); MESILAU CAMP: *RSNB 5858* (K, L); MESILAU RIVER: 1500 m, *RSNB 4211* (K, L, SING), 1500 m, *RSNB 7031* (K, L, SING), 1500 m, *RSNB 7102* (K, L, SING), 1500 m, *de Laubenfels P 622* (L), 1500 m, *P 623* (L); PARK HEADQUARTERS/POWER STATION: 1600 m, *Cockburn & Aban SAN 82967* (K, L); PINOSUK PLATEAU: 1500 m, *Sadau SAN 49689* (L); TENOMPOK: 1400 m, *Smythies S 10614* (K, L, SING), 1500 m, *Wood & Wyatt-Smith SAN 4500* (L, SING); TENOMPOK/KUNDASANG: 1500 m, *Meijer SAN 20411* (L).

34. GNETACEAE

Markgraf, F. Monographie der Gattung *Gnetum*. Bull. Jard. Bot. Buit., ser. 3, 10: 407–511. 1930. Markgraf, F. Gnetaceae. Fl. Males. I, 4(3): 336–347. 1951. Markgraf, F. Gnetaceae. (Addenda, corrigenda et emendanda). Fl. Males. I, 6: 944–949. 1972.

34.1. Gnetum

34.1.1. Gnetum cuspidatum Blume, Rumphia 4: 5. 1848. Fig. 22.

Woody climber. Lower montane forest. Elevation: 400–1700 m.

SPECIMENS EXAMINED. KAUNG: 400 m, *Carr SFN 27293* (SING); KILEMBUN BASIN: 1700 m, *Clemens 33671* (BM, L); TENOMPOK: 1400 m, *Clemens 26203* (BM, K, L), 1500 m, *26203b* (K, L).

34.1.2. Gnetum gnemonoides Brongn. in Duperrey, Voy. Coquille, 12. 1829. Fig. 23.

Woody climber with exceptionally large seeds (2.5–3 × 4.5–6 cm). Lowlands. Elevation: 600 m.

SPECIMENS EXAMINED. PINAWANTAI: 600 m, *Shea & Aban SAN 76917* (K, SING).

34.1.3. Gnetum klossii Merr. ex Markgraf, Bull. Jard. Bot. Buit., ser. 3, 10: 478, t. 11, f. 68. 1930. Figs. 24, 25.

Large woody climber. Hill forest. Elevation: 900 m.

SPECIMENS EXAMINED. DALLAS: 900 m, *Clemens 26003* (K, L), 900 m, *26003b* (K), 900 m, *27021* (K, L), 900 m, *27022* (BM).

34.1.4. Gnetum latifolium Blume, Tijd. Nat. Geschied. & Phys. 1: 160. 1834.

34.1.4a. Gnetum latifolium var. **latifolium.** Fig. 26.

Large woody climber. Lower montane forest. Elevation: 1200–1500 m.

SPECIMENS EXAMINED. BAMBANGAN RIVER: 1500 m, *RSNB 4629* (K, L, SING); MESILAU CAMP: 1300 m, *Meijer SAN 38567* (L); MESILAU RIVER: 1500 m, *RSNB 4229* (K, L, SING); PENIBUKAN: 1200–1500 m, *Clemens 30764* (K, L); SOSOPODON: *Sinanggul SAN 47907* (K, L).

34.1.4b. Gnetum latifolium var. **minus** (Foxw.) Markgraf, Bull. Jard. Bot. Buit., ser. 3, 10: 463. 1930. Fig. 27.

Woody climber. Hill forest, lower montane forest. Elevation: 900–1800 m.

SPECIMENS EXAMINED. DALLAS/BONGOL: 900 m, *Clemens 27645* (BM, L); GURULAU SPUR: 1500 m, *Clemens 50509* (BM, K, L); TENOMPOK: 1200 m, *Clemens 26826* (BM, L, SING), 1500 m, *27506* (BM, K), 1500 m, *27764* (BM, K, L); TINEKUK FALLS: 1800 m, *Clemens 40875* (BM, K, L).

34.1.5. Gnetum leptostachyum Blume, Rumphia 4: 5. 1848.

34.1.5a. Gnetum leptostachyum var. **leptostachyum.** Figs. 28, 29.

Woody climber. Hill forest, lower montane forest. Elevation: 600–1500 m.

SPECIMENS EXAMINED. DALLAS: 900 m, *Clemens s.n.* (BM), 900–1200 m, *26246* (BM, K, L), 900 m, *26264* (L), 900 m, *26284* (K), 900 m, *26429* (BM, K), 900 m, *26598* (K, L), 900 m, *26672* (BM, K, L), 900 m, *26698* (BM, K, L), 900 m, *26710* (BM, K, L), 900 m, *26848* (BM, K), 900 m, *27034* (K), 900 m, *27356* (L), 900 m, *27597* (K), 900 m, *27643* (BM, K), 900 m, *30311* (K, L); DALLAS/TENOMPOK: 1200 m, *Clemens 27597* (BM); GURULAU SPUR: 1500 m, *Clemens 51039* (BM, K, L); KAUNG: 800 m, *Mujin SAN 26759* (K, L); LIWAGU/MESILAU RIVERS: 1200 m, *RSNB 2595* (K, L, SING), 1200 m, *RSNB 2600* (K, L); LOHAN RIVER: 700–900 m, *Beaman 9242* (K, MSC); LOHAN/MAMUT COPPER MINE: 900 m, *Beaman 10640a* (K, MSC), 1000 m, *10645* (K, MSC); MARAI PARAI: 1500 m, *Clemens 33072* (BM, K, L); MINITINDOK GORGE: 900–1200 m, *Clemens 29670* (BM); MT. NUNGKEK: 900–1200 m, *Clemens 32728* (BM, L, SING); PORING

Hot Springs: 600 m, *Beaman 7545* (MSC); Poring Hot Springs/Langanan Water Falls: 600–1000 m, *Kokawa & Hotta 4904* (L); Singh's Plateau: 1000 m, *Meijer SAN 26418* (K, L, SING); Sosopodon: 1200 m, *Mikil SAN 37711* (K); Tenompok: *Clemens 27532* (BM, K, L), 1500 m, *29670* (K, L).

34.1.5b. Gnetum leptostachyum var. **abbreviatum** Markgraf, Reinwardtia 1: 462. 1952.—Type: Marai Parai, 1500 m, *Clemens 32990* (holotype: M?, n.v.; isotypes BM! L!). Fig. 30.

Woody climber. Lower montane forest, mostly on ultramafic substrate. Elevation: 1200–1800 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Kilembun River Head: 1800 m, *Clemens 32475* (BM, K, L); Lumu-lumu: 1600 m, *Carr SFN 27103* (SING); Marai Parai: 1500 m, *Clemens 32276* (BM, L), 1400 m, *32488* (BM, L), 1800 m, *32601* (L), 1200–1500 m, *32698* (L), 1500 m, *32991* (BM, K); Marai Parai Spur: 1800 m, *Clemens 32601* (BM); Marai Parai/Nungkek: 1200–1500 m, *Clemens 32698* (BM); Pinosuk Plateau: *Poore H18* (K, L).

34.1.6. Gnetum neglectum Blume, Rumphia 4: 6, t. 175, f. 2. 1848. Fig. 31.

Woody climber. Hill forest. Elevation: 700–1100 m.

Specimens Examined. Eastern Shoulder: 1100 m, *RSNB 646* (K, SING); Hempuen Hill: *Beaman 7689* (MSC); Kipungit Hill: 700 m, *Beaman 7641* (K, MSC); Lohan River: 800–1000 m, *Beaman 9051* (K, MSC); Melangkap Kapa: 700–1000 m, *Beaman 8788* (K, MSC).

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We are grateful for the opportunities provided by Datuk Lamri Ali, Director of Sabah Parks, to work in Kinabalu Park. Various members of the Park staff, particularly Park Ecologist Jamili Nais, former Park Ecologist Anthea Phillipps, Naturalists Alim Biun and Ansow Gunsalam, and Ranger Gabriel Sinit, were very helpful during our visits.

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RSNB (lower than 2700) under Chew, Corner & Stainton; RSNB (higher than 4000) under Chew & Corner
Sadau 42811 (33.1.1a); 42812 (31.1.3); 42890 (33.1.1a); 49689 (33.6.1).
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Wyatt-Smith 80371 (32.1.1).

FIG. 2. *Agathis borneensis.* Leaves opposite, long-acuminate, parallel-veined; terminal bud globose. (*Beaman 7694,* K.)

FIG. 3. *Agathis kinabaluensis.* Leaves opposite, short-acuminate, parallel-veined; terminal bud globose. (*Beaman 9556,* K.)

FIG. 4. *Agathis lenticulata.* Leaves opposite, hardly if at all acuminate, parallel-veined; terminal bud globose. (*Chew & Corner RSNB 4330,* K.)

FIG. 5. *Phyllocladus hypophyllus.* True leaves absent on mature branches, these replaced by coarsely toothed, pinnately veined cladodes. (*Low s.n.* in 1851, holotype, K; one of the first specimens collected on Mount Kinabalu.)

FIG. 6. *Dacrycarpus imbricatus* var. *patulus*. Leaves strongly dimorphic; juvenile leaves much larger, bilaterally flattened, distichous; adult leaves small, not bilaterally flattened, spirally arranged. (*Sadau SAN 42890*, K.)

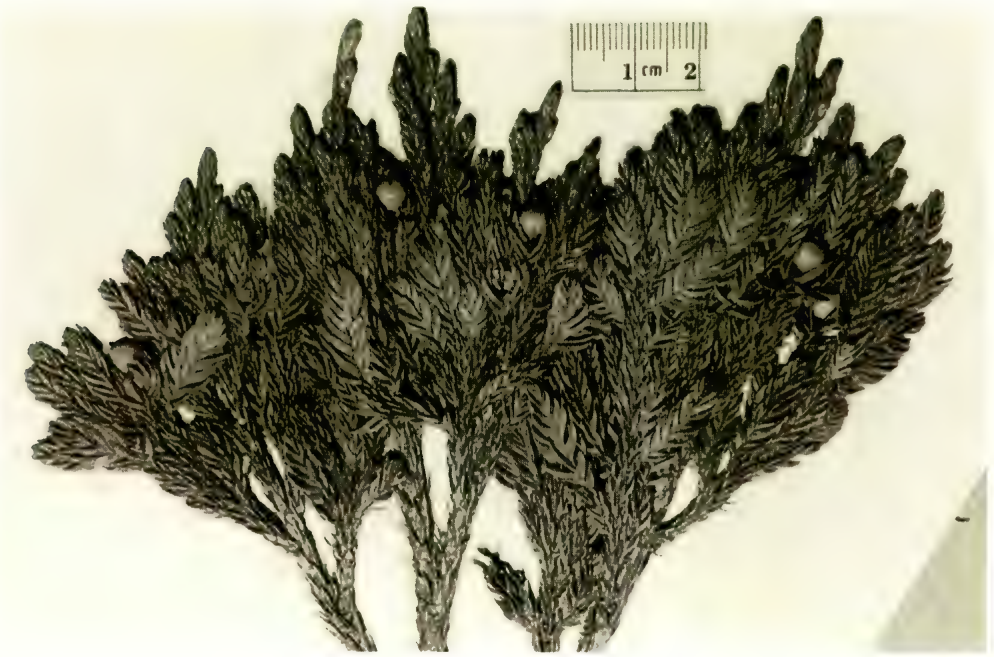

FIG. 7. *Dacrycarpus kinabaluensis*. Leaves dimorphic; juvenile leaves somewhat larger, bilaterally flattened, distichous; adult leaves somewhat smaller, not bilaterally flattened, spirally arranged. (*Chew & Corner RSNB 5887*, K.)

FIG. 8. *Dacrydium beccarii.* Leaves spirally arranged, relatively long, slender, straight, densely disposed on the stems, directed upward. (*Beccari 2385,* isotype, K; from Mt. Poe, Sarawak.)

FIG. 9. *Dacrydium gibbsiae.* Leaves spirally arranged, the longest ca 1 cm long, thick and stiff, curved upward and inward. (*Beaman 8306,* K.)

FIG. 10. *Dacrydium gracilis.* Leaves spirally arranged, the longest mature leaves mostly less than 1 cm long, relatively slender and straight, not extremely dense, directed upward but not stiffly curving inward. (*Cockburn & Aban SAN 82959,* K.)

FIG. 11. *Dacrydium pectinatum.* Leaves spirally arranged, short and stiff, not more than 0.5 cm long on mature branches, directed upward and curving inward. (*Meijer SAN 20970,* K.)

FIG. 12. *Dacrydium xanthandrum.* Leaves spirally arranged, relatively long and slender, ca 1 cm long, not very dense, mostly projecting perpendicular to the stem. (*Meijer SAN 23500,* K.)

FIG. 13. *Falcatifolium falciforme.* Leaves spirally arranged but distichous, bilaterally flattened, single-veined, falcate, variable in size. (*Meijer SAN 20953,* K.)

FIG. 14. *Nageia wallichiana.* Leaves opposite, elliptic, parallel-veined; terminal bud acuminate. (*Aban SAN 62022,* K.)

FIG. 15. *Podocarpus brevifolius.* Leaves spirally arranged, short, mostly 2–3 cm long, densely distributed on the stem, directed upward (in dried material), margin slightly revolute. (*Cockburn & Aban SAN 82276,* K.)

FIG. 16. *Podocarpus confertus.* Leaves spirally arranged or sometimes subopposite, long (ca 6–8 cm), relatively narrow, linear or linear lanceolate. (*Madani SAN 89400,* K.)

FIG. 17. *Podocarpus gibbsii.* Leaves spirally arranged, short, less than 2.5 cm long, oblanceolate, not appearing to be directed upward, margin revolute. (*Clemens 32021,* K, isotype.)

FIG. 18. *Podocarpus globulus.* Leaves spirally arranged or sometimes subopposite, relatively long (ca 7–8 cm), linear. (*De Laubenfels P688,* K, isotype; from Mt. Silam, Sabah.)

FIG. 19. *Podocarpus laubenfelsii.* Leaves spirally arranged, mostly linear-lanceolate, long (8–10 cm or more), unusually wide (sometimes 2 cm or more), acuminate. (*Chew et al. RSNB 2657,* K.)

FIG. 20. *Podocarpus neriifolius.* Leaves spirally arranged, linear, long (often 8 cm or more), acuminate, the blade wrinkled perpendicular to midrib (especially in dried material). (*Chew & Corner RSNB 4255,* K.)

FIG. 21. *Sundacarpus amara.* Leaves spirally arranged, linear or linear-lanceolate, long-acuminate, midvein longitudinally grooved above. (*Cockburn & Aban SAN 82967,* K.)

FIG. 22. *Gnetum cuspidatum.* Leaves opposite, acuminate, coriaceous; seeds sessile, less than 2.5 cm long, surface smooth, on short reproductive branches, borne from collars with thick hair masses. (*Clemens 26203*, K.)

FIG. 23. *Gnetum gnemonoides.* Leaves opposite, ovate, acuminate; seeds 4.5–6 cm long. (*Shea & Aban SAN 76917*, K.)

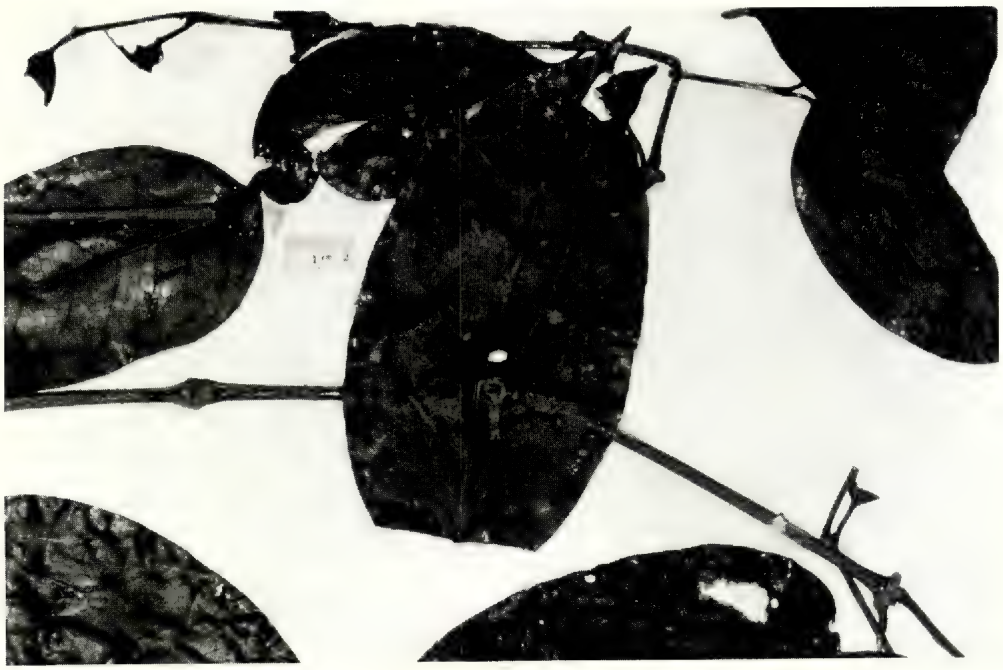

FIG. 24. *Gnetum klossii.* Leaves opposite, ovate-elliptic, acuminate, coriaceous. (*Clemens 26003,* K.)

FIG. 25. *Gnetum klossii.* Seed surface roughened by wavy warts, brown; ♀ reproductive branches similarly roughened. (*Clemens 27021,* K.)

FIG. 26. *Gnetum latifolium* var. *latifolium*. Leaves opposite, ovate to narrowly ovate, coriaceous, mostly longer than 9 cm; seeds distinctly stalked, surface smooth (but wrinkled in dried material). (*Chew & Corner RSNB 4629*, K.)

FIG. 27. *Gnetum latifolium* var. *minus*. Leaves opposite, elliptic, short-acuminate, coriaceous, short, not longer than 9 cm; seeds distinctly stalked, surface smooth (but wrinkled in dried material). (*Clemens 27506*, K.)

FIG. 28. *Gnetum leptostachyum* var. *leptostachyum.* Leaves opposite, elliptic-oblong, coriaceous, ca 20 cm or more long. (*Mujin SAN 26759,* K.)

FIG. 29. *Gnetum leptostachyum* var. *leptostachyum.* Reproductive shoots several-branched; seeds sessile, surface smooth (but somewhat wrinkled in dried material). (*Mujin SAN 26759,* K.)

FIG. 30. *Gnetum leptostachyum* var. *abbreviatum.* Leaves opposite, elliptic-oblong, coriaceous, not more than 12 cm long. (*Clemens 32475,* K.)

FIG. 31. *Gnetum neglectum.* Leaves opposite, lanceolate-elliptic or oblong, relatively thin. ♀ reproductive shoots short, unbranched or nearly so; seeds sessile, small, less than 2 cm long, surface smooth, borne from collars with thick hair masses. (*Beaman 7641,* K.)

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CHROMOSOME NUMBERS OF NEOTROPICAL MALPIGHIACEAE

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For some years I have been accumulating meiotic chromosome counts for neotropical Malpighiaceae, as time and materials made that possible. Some of those counts have been reported by me and my associates in scattered revisionary publications; the rest have never been published, and a number of those are the first counts in their genus. My purpose here is to report all those numbers in one place, and to comment on the systematic implications of some of them. This paper does not pretend to list all the chromosome numbers that have been published for neotropical Malpighiaceae, principally because I have not had the opportunity to verify the identity of the vouchers for most of those counts; some of those vouchers probably do not exist. However, I have included in Table 1 a few counts made and published by others but vouchered by specimens whose identification I have verified, plus one count whose voucher, although currently unavailable for verification, I am reasonably confident was identified correctly.

All of the counts made at the University of Michigan are from pollen mother cells undergoing meiosis; the pairs of chromosomes were stained in the usual acidic preparation with carmine or orcein and counted in squashed cells. Except where a publication is cited in a footnote, all these counts were made by me or Bronwen Gates, who did a number of chromosome counts, especially in the genus *Banisteriopsis*, when she was working in Malpighiaceae under my direction. All of the vouchers cited are deposited in the University of Michigan Herbarium (MICH) except where some other herbarium is cited. Where two or more vouchers are cited, that species was counted independently in material from each voucher. Except for cases where the voucher is followed by an asterisk (*), all of the counts made at the University of Michigan are documented by permanent microscope slides in my personal collection, which will afford the possibility of re-study and correction in the case of counts that might come into question. A star (★) denotes a collection for which I made the count in buds from greenhouse-grown plants derived from the voucher; all other counts made at Michigan were from buds collected from the original voucher.

DISCUSSION

Subfamily Byrsonimoideae

When I proposed this subfamily (W. Anderson 1978), I used as one of the bases for the group its possession of chromosome numbers of $n = 6$ or multiples of 6. That generalization continues to be supported by most, but not all, of the counts recorded in Table 1. The genera cited in Table 1 that I would place in subfamily Byrsonimoideae are *Blepharandra*, *Byrsonima*, *Diacidia*, *Galphimia*, *Lophanthera*,

TABLE 1. Chromosome numbers of neotropical Malpighiaceae.

Genus + species	*n*	Voucher
Aspicarpa		
brevipes (DC.) W. R. Anderson	40	Anderson & Laskowski 3668★
harleyi W. R. Anderson	40	Anderson 11758
humilis Benth.[1]	40	Anderson & Laskowski 3584★
hyssopifolia A. Gray	40	Anderson 13321
pulchella (Griseb.) O'Don. & Lourt.	40	Anderson 11173
schininii W. R. Anderson	20	Anderson 11777
Banisteriopsis		
acapulcensis var. *llanensis* B. Gates	10	Gates 307*
acerosa (Nied.) B. Gates	10	Anderson 11177
andersonii B. Gates	10	Gates 351
angustifolia (Adr. Juss.) B. Gates	10	Anderson 11592; Gates 348
argyrophylla (Adr. Juss.) B. Gates	10	Anderson 11142; Gates 399
campestris (Adr. Juss.) Little	10	Gates 357
cipoënsis B. Gates	10	Gates 386
hypericifolia (Adr. Juss.) W. R. Anderson & B. Gates	10	Anderson 11548*
laevifolia (Adr. Juss.) B. Gates	10	Anderson 11143
muricata (Cav.) Cuatr.	20	Anderson 11148
oxyclada (Adr. Juss.) B. Gates	10	Anderson 11144
pulchra B. Gates var. *pulchra*	10	Anderson 11789
valvata W. R. Anderson & B. Gates	10	Anderson 12500
vernoniifolia (Adr. Juss.) B. Gates	10	Anderson 11490
Barnebya		
harleyi W. R. Anderson & B. Gates	(29) 30[2]	Guidon 2926
Blepharandra		
hypoleuca (Benth.) Griseb.	12	Holst 3839
Bunchosia		
montana Adr. Juss.	20	Anderson 13123
Byrsonima		
basiloba Adr. Juss.	12	Anderson 11423
crassifolia (L.) H. B. K.	12	Bawa 118 (MO)[3]
macrophylla (Pers.) W. R. Anderson	12	Anderson 11565
oblongifolia Adr. Juss.	12	Anderson 11496
rigida Adr. Juss.	12	Anderson 11371
sericea DC.	12	Anderson 7630
Callaeum		
macropterum (DC.) D. M. Johnson	10	Daniel 1941[4]
septentrionale (Adr. Juss.) D. M. Johnson	10	Anderson & Laskowski 4046
Camarea		
affinis St.-Hil.	17	Anderson 11243
axillaris St.-Hil.	17	Anderson 9012
ericoides St.-Hil.	17	Anderson 11443 (NY), 11497
hirsuta St.-Hil.	17	Anderson 6849, 7948
Cordobia		
argentea (Griseb.) Nied.	9	Anderson 12359
Diacidia		
rufa (Maguire) W. R. Anderson	(23) 24[5]	Anderson 13373
Dicella		
bracteosa (Adr. Juss.) Griseb.	10	Anderson 11761
Echinopterys		
eglandulosa (Adr. Juss.) Small	10	Cochrane & Cochrane 8505
eglandulosa (Adr. Juss.) Small	20	Daniel 3359
Ectopopterys		
soejartoi W. R. Anderson	8	Soejarto et al. 4416

TABLE 1 continued.

Galphimia		
angustifolia Benth.	12	Lynch 710 (MO)[6]
glauca Cav.	6	Anderson 13555; Breedlove 7072 (CAS)[7], 19114 (CAS)[8]
gracilis Bartl.	12	Fryxell & Anderson 3484; MacBryde & Herrera-MacBryde 63 (MO)[6]
Gaudichaudia		
albida Schlecht. & Cham. sens. str.	40	Anderson & Laskowski 4259★; Anderson 13198
albida Schlecht. & Cham. sens. lat.	40	Anderson & Laskowski 3844#2★, 4147★, 4467★; Anderson 13216, 13224; Koch & Fryxell 83253
chasei W. R. Anderson	40	Anderson 12945
cycloptera (DC.) W. R. Anderson	40	Anderson & Laskowski 3669★, 4545★*
cynanchoides H. B. K.	40	Anderson 12642
diandra (Nied.) Chodat	40	Anderson 13309; Daniel & Butterwick 3257
galeottiana (Nied.) Chodat	40	Anderson & Laskowski 4087★
krusei W. R. Anderson	40	Anderson 12868
mcvaughii W. R. Anderson	40	Anderson 12699
subverticillata Rose	40	Anderson & Laskowski 3698★
sp. aff. *cynanchoides* H. B. K.	80	Anderson & Laskowski 3645★; Anderson 12624
sp. aff. *cycloptera* (DC.) W. R. Anderson	80	Anderson & Laskowski 3925★; Anderson 13265
sp. aff. *diandra* (Nied.) Chodat	80	Anderson 12937
sp.	80	Anderson & Laskowski 3707★, 3714★, 4293★; Anderson 12990, 13031, 13148, 13316; Rzedowski 32522★
sp.	120	Anderson & Laskowski 4056★
Heteropterys		
byrsonimifolia Adr. Juss.	10	Anderson 11571
campestris Adr. Juss.	10	Anderson 11450, 11517
coleoptera Adr. Juss.	10	T. A. Silva 02 (R)[9]
escalloniifolia Adr. Juss.	10	Anderson 11531
sericea (Cav.) Adr. Juss. in St.-Hil.	10	Anderson 11578
Janusia		
anisandra (Adr. Juss.) Griseb.	40	Anderson 9180, 11755
californica Benth.	10	Anderson 12553, 12539; Daniel 3373
gracilis A. Gray	20	Anderson & Laskowski 3520★, 4558★, 4559★
guaranitica (St.-Hil.) Adr. Juss.	19	Anderson 11136, 11174, 11176
janusioides (Adr. Juss.) W. R. Anderson sens. str.	20	Anderson 12517
janusioides (Adr. Juss.) W. R. Anderson sens. lat.	20	Anderson 11313
lindmanii (Skottsb.) W. R. Anderson	20	Anderson 10614, 11090
linearis Wiggins	10	Anderson 12551
mediterranea (Vell.) W. R. Anderson	20	Anderson 7752, 11183
occhionii W. R. Anderson	20	Anderson 11151, 11175
prancei W. R. Anderson	20	Anderson 12334
schwannioides W. R. Anderson	20	Anderson 12514
Jubelina		
magnifica W. R. Anderson	10	Anderson 13361

TABLE 1 concluded.

Lophanthera		
hammelii W. R. Anderson	6	Schatz 1034[10]
lactescens Ducke	6	Anderson 11665
Malpighia		
glabra L.	10	Bawa 163 (MO)[11]
Mascagnia		
cordifolia (Adr. Juss.) Griseb.	20	Anderson 11246
polybotrya (Adr. Juss.) Nied.	10	Anderson 12944
Mcvaughia		
bahiana W. R. Anderson	10	Anderson 11740
Peixotoa		
glabra Adr. Juss.	10	Anderson 11549
hispidula Adr. Juss.	10	T. A. Silva 01[9]
reticulata Griseb.	[15][12]	Anderson 11790
Peregrina		
linearifolia (St.-Hil.) W. R. Anderson	19	Anderson 11764
Pterandra		
egleri W. R. Anderson	12	Anderson 10895
Stigmaphyllon		
jatrophifolium Adr. Juss.	10	Anderson 12371
lalandianum Adr. Juss.	10	Anderson 11610, 11666
paralias Adr. Juss.	10	Ormond 650[9]
retusum Griseb.	10	Fryxell & Anderson 3485
Thryallis		
longifolia Mart.[13]	(29) 30[2]	Anderson 12515
Verrucularia		
glaucophylla Adr. Juss.	6	Anderson 13704

[1]The taxonomy of *Aspicarpa* in North America is not fully resolved, and it is possible that *A. humilis* will ultimately fall into synonymy under *A. hirtella* L. C. Rich.

[2]The best figures indicate that the correct count is 30, but it is possible that I am consistently misinterpreting as two one pair whose halves are very loosely associated in late prophase.

[3]Bawa 1973.

[4]Baker & Parfitt 1986, under the name *Mascagnia macroptera*.

[5]No perfect figures were found. The best figures available show that n = at least 23, and probably 24.

[6]MacBryde 1970.

[7]Kyhos 1966.

[8]Seavey 1975.

[9]Ormond et al. 1981.

[10]This count was made on buds of *Hammel 13339*, of which the voucher specimens were subsequently lost. *Schatz 1034* is a fruiting specimen that was made later from the same tree as *Hammel 13339*, and can therefore serve as a voucher for this chromosome count.

[11]Bawa 1973; voucher unavailable for verification.

[12]Meiosis is highly irregular, with anaphase figures only occasionally 15+15, more often 14+16 or 13+17. This species is probably a substerile triploid; most seed-set is apparently apomictic. See C. Anderson, 1982, pp. 65–66.

[13]The taxonomy of *Thryallis* needs study. This specific epithet is applied provisionally, with the understanding that the voucher may prove to represent an undescribed species when the genus is revised.

Mcvaughia, *Pterandra*, and *Verrucularia*. With one exception all the numbers in Table 1 for those genera are 6, 12, or 24. The exception is *Mcvaughia bahiana*, which has $n = 10$, the number characteristic of subfamily Malpighioideae. Nevertheless, I remain quite convinced that *Mcvaughia* belongs in subfamily Byrsonimoideae, for the reasons advanced when it was described (W. Anderson 1979), and I can only suppose that $n = 10$ in this genus was derived independently by aneuploid reduction from $n = 12$. Unfortunately we still have no count for *Burdachia*, the probable sister-genus of *Mcvaughia*.

The number $n = 6$ is the lowest known for the Malpighiaceae, and seems likely to be basal in the family (W. Anderson 1983). The plants showing that number are assignable to *Galphimia*, *Lophanthera*, or *Verrucularia*, all of which I placed in tribe Galphimieae in 1978. As I have recently pointed out (W. Anderson 1990b), *Lophanthera* and *Verrucularia* share several plesiomorphic morphological characters which, taken with their low chromosome numbers, suggest that they may be near the base of the phylogeny of the family. In the light of these observations it would be especially interesting to learn chromosome numbers for *Spachea*, the fourth genus of Galphimieae.

Anderson and Gates (1981) considered *Barnebya* to be fairly closely related to the Byrsonimoideae, in spite of its having winged fruits that resemble those common in subfamily Malpighioideae. The relationships of this problematic genus are not clarified by its chromosome number, which seems to be $n = 30$. That number is a multiple of both 6, which is basal in the Byrsonimoideae, and 10, which is basal in Malpighioideae, but in neither case can I postulate derivation of 30 through a series of doublings. *Barnebya* remains an intriguing enigma.

Subfamily Malpighioideae

Most of the remaining genera in Table 1 form a more or less natural group, which must take the name Malpighioideae because it includes *Malpighia*, the type of the family. The group is characterized by derived pollen, winged fruits, a climbing habit, and a chromosome number based on $n = 10$, although all of these generalizations are contradicted by one or another of the genera listed here. *Banisteriopsis*, *Callaeum*, *Echinopterys*, *Heteropterys*, *Jubelina*, *Mascagnia*, *Peixotoa*, and *Stigmaphyllon* all fit fairly comfortably into this group and I shall say little more about them; their chromosome numbers are monotonously uniform, with only rare departures from diploid ($n = 10$) to tetraploid ($n = 20$), and therefore not very informative. *Aspicarpa*, *Camarea*, *Gaudichaudia*, *Janusia*, and *Peregrina* make up the tribe Gaudichaudieae, which is derived from *Banisteriopsis* and therefore clearly belongs in this subfamily too; this group is discussed in more detail below. *Cordobia* and *Ectopopterys* are wing-fruited vines which, on the basis of their morphology, I place with confidence in this subfamily. They are not closely related to each other, so I interpret their chromosome numbers ($n = 9$ and 8, respectively) as independently derived through aneuploid reduction from ancestors with $n = 10$. *Malpighia* is derived in having a shrubby habit and fleshy fruits, but the pyrenes of the fruit show rudimentary winglets under the fleshy exocarp, and as I have said before (most recently in 1990a, pp. 50–51), *Malpighia* is so close to *Mascagnia* in most aspects of its morphology that it becomes increasingly difficult to maintain the two as separate genera, so *Malpighia* certainly must go into this subfamily with *Mascagnia*. Its chromosome number ($n = 10$) supports that placement.

The genera that remain unmentioned are *Bunchosia*, *Dicella*, and *Thryallis*, all of which I considered to have more or less uncertain affinities in 1978. At that time I was willing to assert that *Dicella*, in spite of its unwinged fruit, "certainly belongs with other vining genera. . . ." The chromosome number now available, $n = 10$, strengthens that claim, and for now, at least, I am content to leave *Dicella* in the Malpighioideae.

Bunchosia is a genus of trees and shrubs with fleshy fruits of a structure unique in the family. In 1978 I pointed out that *Bunchosia* shares a number of character-states with *Heladena*, a genus of vines bearing dry, unwinged, indehiscent cocci, and Lowrie (1982) stated that the two genera have very similar pollen. If that relationship is supported by additional evidence, and if *Heladena* is to be classified with other genera of vines with dry fruits, then *Bunchosia* may have to remain in the Malpighioideae, anomalous though it seems in that assemblage. The chromosome number reported here, $n = 20$, is consistent with such a disposition; no count has been reported for *Heladena*.

Thryallis, like *Barnebya*, remains an unsolved puzzle. As I noted in 1978, its habit, pollen, and stigmas suggest derivation from one of the wing-fruited vines that would fall in the Malpighioideae, but its links are not obvious and its unique derived character-states are most impressive. A chromosome number of $n = 30$ is as unhelpful as its other autapomorphies. Derivation directly from an ancestor with $n = 10$ or 20 is difficult to postulate, but a hybrid between a diploid and a tetraploid, followed by doubling in the progeny, could produce such an apparent hexaploid. We must hope that molecular studies now under way will shed some light on the relationships of isolated genera like *Thryallis*.

Tribe Gaudichaudieae

Adrien de Jussieu first recognized this group in 1840 and later (1843) refined his concept to one that matches mine, although the generic nomenclature has changed somewhat. I place here the genera *Aspicarpa*, *Camarea*, *Gaudichaudia*, *Janusia*, and *Peregrina*, all of which are represented in Table 1. These genera share a reduced androecium and a terminal capitate stigma; most members of the tribe have only one style and produce a carpophore at the base of each carpel, and many (some species in every genus except *Peregrina*) produce cleistogamous flowers in addition to chasmogamous flowers (W. Anderson 1980). The group seems likely to have originated in the genus *Banisteriopsis*, which hardly differs from some species of *Janusia* except for possessing a full complement of stamens and, usually, three styles. Chromosome numbers are much more interesting in this tribe than in most other Malpighiaceae, showing evidence of both aneuploidy and recurrent cycles of polyploidy.

Janusia comprises two rather different groups, approximately 12–15 species in South America (section *Janusia*) and three species in North America (section *Metajanusia* Niedenzu). The latter are all natives of the deserts of northwestern Mexico and the adjacent United States. They are *J. californica* and *J. linearis*, which are both diploid ($n = 10$), and *J. gracilis*, a tetraploid with $n = 20$. The three are very similar morphologically; the diploids have broad and narrow leaves, respectively, and the tetraploid has leaves of intermediate width. It is also intermediate between the diploids in most other characters (Table 2), and has few if any uniquely distinguishing character-states of its own, which leads me to suggest that *J. gracilis* is an allotetraploid derived, perhaps more than once, from a hybrid

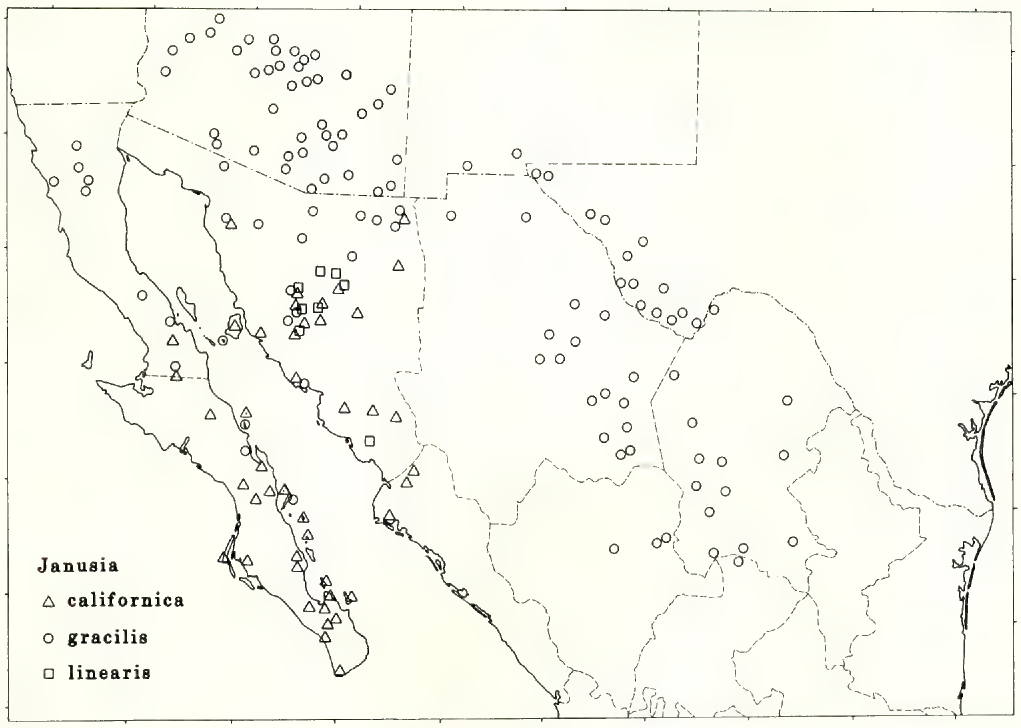

FIG. 1. Distribution of *Janusia* in North America.

between *J. californica* and *J. linearis*. All three species in this little complex occur sympatrically in western Sonora, but the putative allotetraploid has a range that far exceeds the range of either diploid (Fig. 1). Pairing is strictly normal in meiosis in all three species.

TABLE 2. Morphological characters in *Janusia* section *Metajanusia*.

	J. californica	*J. gracilis*	*J. linearis*
Leaf length/width	1.2–2.5	4–10	12–40
Leaf margin	toothed	toothed	entire
Sepal length (mm)	1.7–2.5	2.0–2.5	2.5–3.0
Sepal vesture	glabrous	hairy	hairy
Style length (mm)	1.5–1.9	1.9–2.3	2.1–3.0

The other species of *Janusia* in Table 1 occur in central and southern Brazil, as well as Paraguay, Argentina, and Bolivia. Most have $n = 20$, but *J. guaranitica* has $n = 19$ and *J. anisandra* has $n = 40$. These counts suggest that section *Janusia* is probably a clade based on an ancestor that was already tetraploid relative to $x = 10$ in *Banisteriopsis*, that $n = 19$ in *J. guaranitica* is aneuploid from $n = 20$, and that *J. anisandra* is tetraploid relative to $n = 20$ at the base of the clade. At this time I have no basis for suggesting that the doubling in *J. anisandra* may have been associated with hybridization. All of the species of *Janusia* section *Janusia* that I have studied cytologically show only normal pairing in meiosis.

Aspicarpa and *Camarea* are reduced in both stature and the ornamentation of their fruits. *Camarea* occurs only in southern South America; *Aspicarpa* is both there and in Mexico and the adjacent United States. Plants of both genera are suffruticose or have trailing, almost herbaceous stems from a perennial base; they

usually do not climb, although a few populations in Mexico with very long stems trailing among shrubs show some weak tendency to twine. The ancestral samara as found in *Banisteriopsis* and *Janusia* has been reduced to a nutlet bearing rudimentary winglets or irregular outgrowths. The two genera differ morphologically in the details of their androecia. Chromosome numbers are $n = 20$ or 40 in *Aspicarpa*, 17 in *Camarea*. These suggest that *Aspicarpa* and *Camarea* may have diverged from a common ancestor with $n = 20$, *Camarea* representing a clade set apart by an early aneuploid reduction to $n = 17$, most extant species of *Aspicarpa* being tetraploid relative to that ancestor. Of the species of *Aspicarpa* listed in Table 1, the first, third, and fourth, all tetraploid, are Mexican; the other three, including the only known diploid, are South American from the same area as *Janusia* section *Janusia*.

Peregrina is a monotypic genus of southern Brazil and Paraguay that has a habit and androecium like those of some species of *Aspicarpa* but a samara with a well-developed lateral wing like that found in *Gaudichaudia* (see below). It is obviously close to all of the other genera in the tribe but will not fit happily in any of them, which was my reason for segregating it as a genus (W. Anderson 1985). Its sole species has 19 pairs of chromosomes, presumably through aneuploid reduction from $n = 20$ in an ancestor near the branch from *Janusia* section *Janusia* that gave rise to *Aspicarpa*. It is interesting to note that *Janusia guaranitica* also has $n = 19$, but the two species are otherwise so dissimilar that it would hardly be parsimonious to suggest a close relationship between them; they are much more likely to have reached $n = 19$ through independent reductions.

Genus *Gaudichaudia*

This is a genus of at least ten and perhaps 25 species, mostly Mexican but with a few species extending into Central America and one reaching Colombia and western Venezuela. The genus seems almost certain to have diversified in Mexico, with the plants now in Central America and northwestern South America representing a relatively recent extension of the genus's range southward, not remnants of ancestral immigrants from central or southern South America. Most species of *Gaudichaudia* are vines, but a few are shrubby. They resemble *Janusia* spp. in their androecium and gynoecium, and the well-developed carpophore of their samaras. Most species have the cleistogamous flowers peculiar to this tribe, which are two-carpellate and therefore produce only two samaras, unlike the chasmogamous flowers, which are three-carpellate (W. Anderson 1980). *Gaudichaudia* is distinguished by its eglandular leaves and its samaras, which have the lateral wing well developed and the dorsal wing rudimentary, the opposite of the situation in *Janusia*.

Of the many chromosome numbers now available for *Gaudichaudia*[14], most

[14]In addition to the chromosome counts listed for *Gaudichaudia* in Table 1, I have made a number of attempts that produced figures not good enough to yield a definite count but good enough to tell the approximate ploidy level of the plant. In all my work on this genus, I have seen no evidence of aneuploidy, and I now suspect that all gaudichaudias are euploid. I list here seven very rough counts in *Gaudichaudia*, in the belief that they may be of value to future students of the genus. *Anderson & Laskowski 4236*, diploid, *G. albida* Schlecht. & Cham. sens. str.; *Anderson & Laskowski 4206*, diploid, *G. albida* Schlecht. & Cham. sens. lat.; *Anderson 13285*, diploid, *G. cynanchoides* H. B. K.; *Koch & Fryxell 82218*, diploid, *G. mcvaughii* W. R. Anderson; *Anderson & Laskowski 3926*, tetraploid, *G.* sp. aff. *cycloptera* (DC.) W. R. Anderson; *Anderson 13291*, tetraploid, *G.* sp.; *Anderson 13286*, hexaploid, *G.* sp.

are either $n = 40$ or $n = 80$; $n = 120$ also occurs. I assume that the ancestor of the genus had 40 pairs of chromosomes, tetraploid with respect to some ancestor in *Janusia* section *Janusia* and octoploid relative to a more remote ancestor in *Banisteriopsis*. In the comments that follow I shall use "diploid" to refer to plants with $n = 40$, "tetraploid" for plants with $n = 80$, and "polyploid" for plants with $n =$ either 80 or 120.

The diploids in *Gaudichaudia* are mostly assignable to morphologically recognizable species, which is evident from Table 1. Their fruits include three rather different types, which Niedenzu (1928) used to divide the genus into subgenera and sections, and I shall use the same three sections as a framework for my comments here.

Section *Gaudichaudia* comprises species in which all three samaras from a chasmogamous flower, and both samaras from a cleistogamous flower if such flowers are present, are alike and have a symmetrical orbicular, ovoid, or obovoid shape (Fig. 2a). Of the diploid species in Table 1, the ones that fall in section *Gaudichaudia* are *G. chasei*, *G. cycloptera*, *G. cynanchoides*, *G. krusei*, *G. mcvaughii*, and *G. subverticillata*. *Gaudichaudia chasei*, *G. krusei*, *G. mcvaughii*, and *G. subverticillata* are especially intriguing because they all lack cleistogamous flowers, all produce three styles instead of one, and none is an aggressive colonizer like many gaudichaudias; in addition, *G. krusei* and *G. subverticillata* are small shrubs, not vines. If it were not for the convincing links through *Janusia* to an origin in *Banisteriopsis*, I would suppose three styles and a lack of cleistogamous flowers to be ancestral character-states in this genus, but in the light of what we know about the rest of the tribe that seems unlikely, so perhaps these species represent a clade in which the cleistogamous flowers were lost, probably in correlation with a shift away from weediness, and the three styles of a remote ancestor became able to be expressed once again. The other two species in Table 1, *G. cycloptera* and *G. cynanchoides*, bear cleistogamous flowers and are more aggressive plants, but rather different in their ecology, with *G. cycloptera* more likely to found in mesic places and *G. cynanchoides* often, but not always, found in drier and more disturbed shrubby habitats.

Section *Zygopterys* (Nied.) Nied. contains the single species *G. galeottiana*. As in the preceding section the samaras of a fruit are all symmetrical and alike, but in this case their shape is rather different. It is more or less Y-shaped, with three rounded lobes, two upper and one lower, with a deep division between the two upper lobes and a constriction at the waist between the lower lobe and the two upper lobes (Fig. 2b). This section can be seen as intermediate between the other two; it resembles section *Gaudichaudia* in having all the samaras of a fruit alike, but its samara is somewhat like the anterior samara of section *Tritomopterys* in shape. *Gaudichaudia galeottiana* is a weedy species of dry habitats, and relies heavily on cleistogamous flowers for seed set.

Section *Tritomopterys* Adr. Juss. includes *G. albida* and several closely related species whose taxonomy is not yet fully resolved, as well as *G. diandra*. All the plants in this section have both chasmogamous and cleistogamous flowers, and they are often more or less weedy. The three samaras of a chasmogamous flower are all different. The one from the anterior carpel, which lies on the flower's plane of symmetry, is V- or Y-shaped, with the upper lobes longer and more tapered than in *G. galeottiana* and the lower lobe relatively less developed. The samaras coming from the two lateral carpels of the same flower are one-sided, having the anterior upper lobe of the wing well developed and the other rudimentary or undeveloped. The two lateral samaras are mirror-images of each other, i.e., one

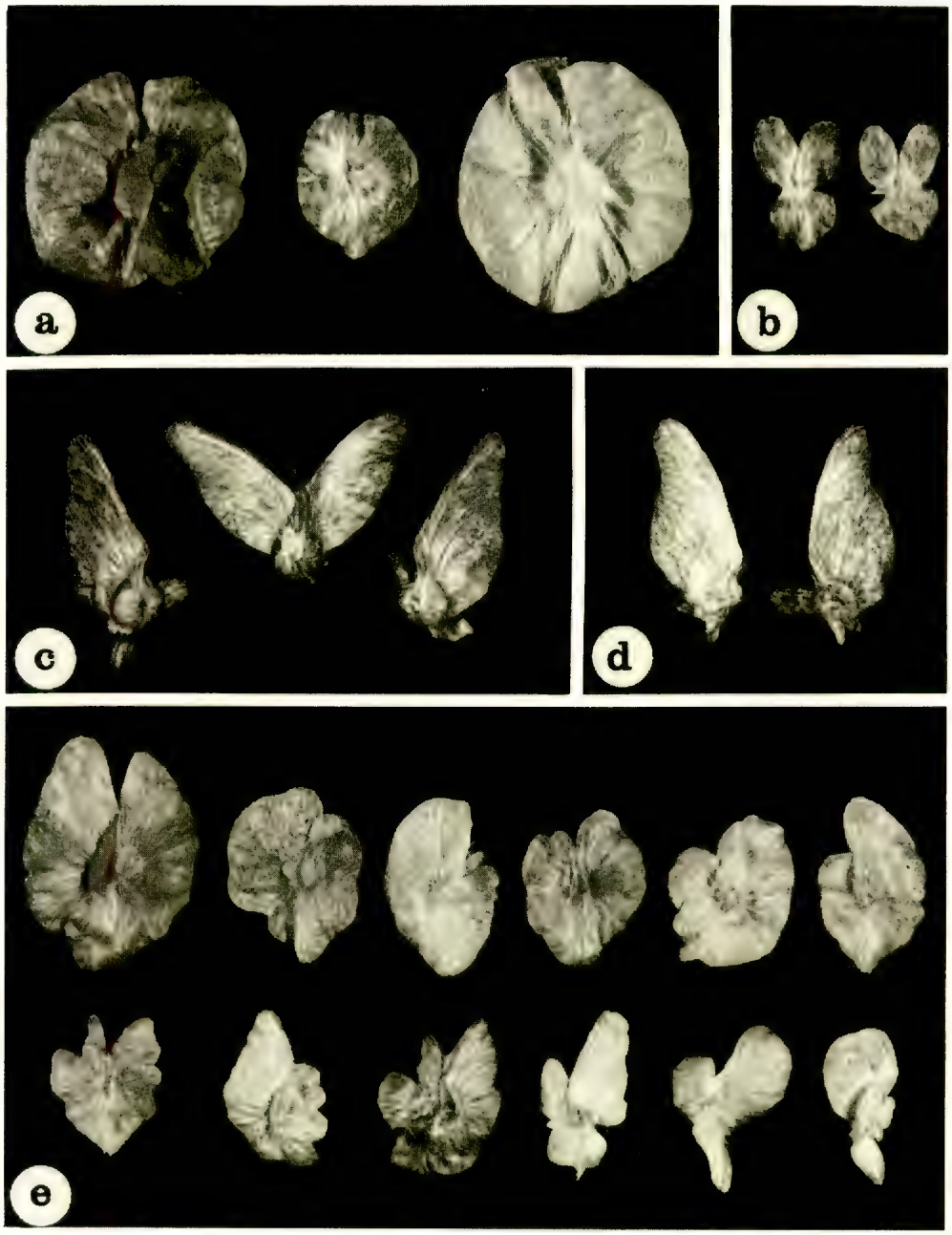

FIG. 2. Samaras of *Gaudichaudia*, all × 1.75. a, section *Gaudichaudia*; left to right: *G. mcvaughii* (*A 12699*, from a chasmogamous flower), *G. cynanchoides* (*A 13285*, from a cleistogamous flower), *G. cycloptera* (*A & L 4510*, from a cleistogamous flower). b, section *Zygopterys*, *G. galeottiana* (*A & L 4087*, both from cleistogamous flowers). c & d, section *Tritomopterys*, *G. diandra* (*A & L 3649*); c, three samaras from a single chasmogamous flower, the central one from the anterior carpel; d, two samaras from a single cleistogamous flower. e, known or probable polyploids, *G.* spp.; upper row, left to right: *A 13291*, *A 13031*, *A 12661*, *A & L 4108#5*, *A 13316*, *A 12624*; lower row, left to right: *A & L 4293*, *A & L 4056*, *A & L 3867*, *A 13320*, *A 13138*, *A 12990*; all from cleistogamous flowers. Abbreviations of collectors: *A* = *Anderson*; *A & L* = *Anderson & Laskowski*.

has its right side developed and the other has its left side developed (Fig. 2c). As noted above, the cleistogamous flowers in this tribe usually have only two carpels, and the one that is missing is the anterior carpel, so as one might expect, the two samaras produced by a cleistogamous flower in species of section *Tritomopterys* are one-sided (Fig. 2d).

If that were all one encountered in *Gaudichaudia* there would be no great difficulty to its systematics, but in fact many plants will not fit into one of the three morphologically defined sections. It is common to find populations whose fruits are extremely variable and intermediate between the three sections that accommodate the diploid species. These fruits range from being very close to those of section *Gaudichaudia* through every conceivable degree of lobing to ones that are very close to those of section *Tritomopterys*, and in some cases one can find a large portion of that spectrum of variation in a single population, and even on a single plant (Fig. 2e). These plants with intermediate fruits are always vines, they always bear cleistogamous as well as chasmogamous flowers, and they are often aggressive weeds, being especially common in shrubs in overgrazed pastures and along disturbed roadsides. In every case where I have been able to count the chromosomes of plants with such intermediate samaras they have been polyploids, mostly tetraploid with $n = 80$, occasionally hexaploid with $n = 120$ (see Table 1). This correlation between morphology and ploidy level has led me to the obvious hypothesis that the polyploids with intermediate fruits have resulted from hybridization between the diploids with consistent fruits. That hybridization may have happened at the diploid level, followed by restoration of fertility to sterile hybrids through doubling of the chromosomes. These plants would be preadapted for such a scenario through possession of cleistogamous flowers. A single tetraploid plant could produce large quantities of samaras through self-fertilization in the cleistogamous flowers, and thus have a much higher probability of surviving than must usually be the case when a single tetraploid appears among a swarm of diploid hybrids. It is also possible that hybridization has occurred at the tetraploid level, between autotetraploids arising spontaneously among the diploids. That would be consistent with the fact that some tetraploids are morphologically nearly indistinguishable from diploids, and it would help to explain why the variation among the fruits fills the gaps between the diploids so completely, because tetraploid hybrids derived from tetraploid "species" should be able to backcross freely to their parents. The cytological history of the tribe Gaudichaudieae, as reviewed above, suggests that autopolyploidy followed by complete diploidization has happened repeatedly in this group of plants. I have certainly seen no sign of reproductive irregularity in any plant of *Gaudichaudia*; pairing is always perfect at meiosis, fruit-set is heavy, and germination of the fruits is ready and abundant.

The sections of *Gaudichaudia* are not evenly distributed through Mexico (Fig. 3). Section *Gaudichaudia* is mostly central and western, section *Zygopterys* has a restricted distribution in Puebla and Oaxaca, and section *Tritomopterys* extends south and east from western and eastern Mexico, but avoiding the driest part of the Central Plateau, throughout southern Mexico and into Central America and northwestern South America. Sections *Gaudichaudia* and *Zygopterys* are not sympatric, but section *Tritomopterys* has large areas of sympatry with both of them, and of course we have no way of knowing what the distributions of these groups may have been in past times. When we look at the distribution of the probable diploids as compared to the distribution of probable polyploids (Fig. 4), we find that they co-occur today over much of south-central Mexico, but the polyploids

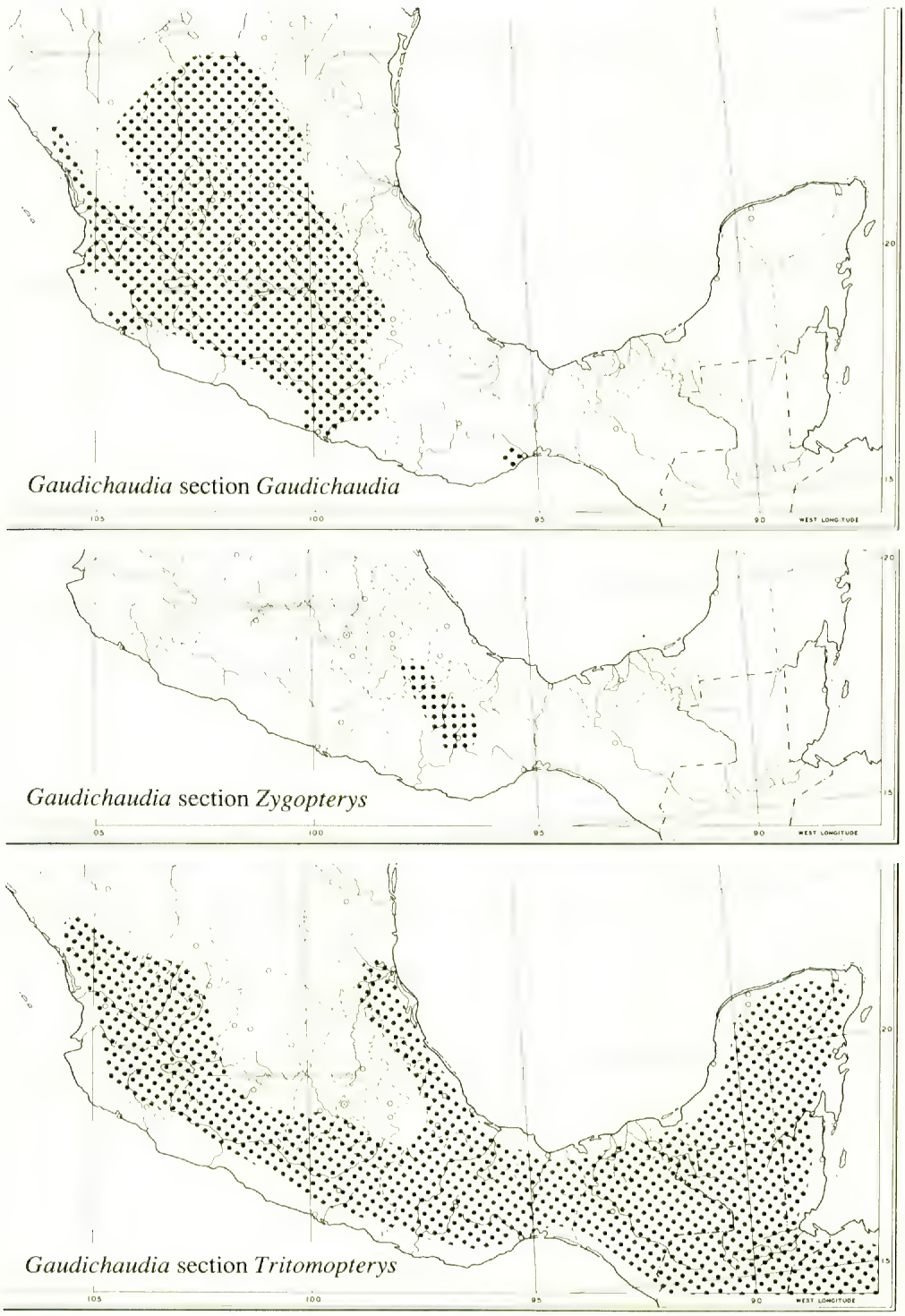

FIG. 3. Distribution of the sections of *Gaudichaudia*; not shown is the continuation of section *Tritomopterys* through Central America into northwestern South America.

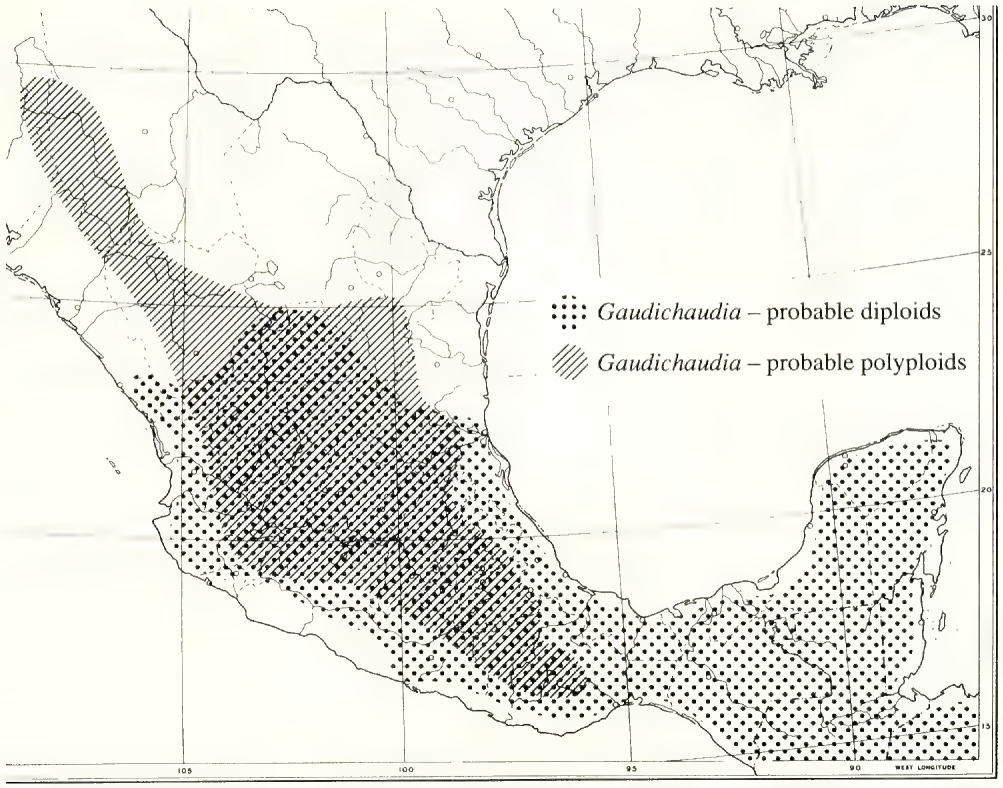

FIG. 4. Distribution of *Gaudichaudia* in Mexico.

have expanded farther north into Mexico than any diploid, and there is no hint from morphology that any of the plants found east and south of the Isthmus of Tehuantepec are likely to be polyploids or of hybrid origin.

Chromosome numbers in *Gaudichaudia* have pointed the way toward at least a preliminary understanding of a very complex situation. It seems likely that frequent hybridization has produced the morphological complexity and that polyploidy plays an essential role in the stabilization of those hybrids. Cleistogamous flowers, which were presumably an earlier adaptation for a pioneer habit, probably facilitated the survival of polyploids, and the chasmogamous flowers, which keep some outcrossing available even to plants which depend mostly on cleistogamy for seed-set, enabled backcrossing and further rounds of hybridization, with each new fertile hybrid able to perpetuate itself indefinitely through self-fertilization in the cleistogamous flowers. This process may well be continuing today. It would be especially interesting to investigate the relationship between an aggressively colonizing habit, disturbance caused by humans, and the evolution of the many populations of putative hybrids. It may be that there is a tight correlation between such recent disturbance and the success of these hybrids, and that the hybrids cannot persist in the absence of such disturbance. As for the systematics of the polyploids, that is still to be resolved, as is evident from Table 1. Given their excessive variability, it will probably never be possible to divide them up into the kind of tidy species that taxonomists prefer. We may have to recognize several broadly-defined taxa of convenience, based perhaps on a few relatively reliable characters and our best understanding of their probable origins. Much remains to be done in this perplexing genus.

ACKNOWLEDGMENTS

Bronwen Gates contributed both counts and preparations for subsequent counting by me, and I am grateful for her cheerful assistance. George Rogers photographed the samaras of *Gaudichaudia diandra*. This work was supported by a series of grants from the National Science Foundation to the University of Michigan and, before that, to the New York Botanical Garden; the most recent such grant was BSR-8700340 to the University of Michigan. The following colleagues sent buds fixed in the field for study in Ann Arbor or fruits for cultivation, and I send special thanks to all of them: T. S. Cochrane, T. F. Daniel, L. Emperaire, P. A. Fryxell, B. E. Hammel, B. K. Holst, S. D. Koch, J. Rzedowski, and D. D. Soejarto.

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NOTES ON NEOTROPICAL MALPIGHIACEAE—IV

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The notes that follow are a true miscellany, published here for diverse reasons. It would be much better, of course, if they could appear in the context of complete monographic treatments of these groups, but monographs of large genera like *Bunchosia*, *Byrsonima,* and *Heteropterys* are years in the future, and much of what follows cannot wait that long. Several of the new species are needed for floras, or have already been cited as *nomina nuda* in floristic lists. In other cases, notes of explanation are needed for actions taken or soon to be taken; for example, non-specialists seeing my recent annotations on specimens may reasonably wonder why I have abandoned a well-established name like *Heteropterys beecheyana* Adr. Juss. for *H. brachiata* (L.) DC., and why I am using *Mascagnia divaricata* (H. B. K.) Nied. for the species traditionally called *M. ovatifolia* (H. B. K.) Griseb. Moreover, a number of the entries supplement Niedenzu's 1928 monograph by clarifying problems that he had to leave unresolved, usually because he did not have the opportunity to study critical collections in Paris and London. I trust that the relevance of each entry will be obvious to informed readers.

Bunchosia itacarensis W. R. Anderson, sp. nov.—TYPE: BRAZIL. Bahia: Mun. Itacaré, 3 km S of Itacaré, forest at edge of ocean, Dec fl, *Mori et al. 13081* (holotype: MICH!; isotypes: CEPEC, NY, not seen).

Frutex vel arbor parva 2–3 m alta, ramis permox glabratis. Lamina foliorum majorum 14–21 cm longa, 6.7–9.2 cm lata, permox glabrata, abaxialiter biglandulosa prope basim; petiolus 10–12 mm longus eglandulosus; stipulae 2–3 mm longae. Inflorescentia saepe ternata. Sepala utrinque glabra, margine saepe ciliata. Gynoecium bicarpellatum; ovarium dense sericeum; styli 2, 1.4 mm longi, liberi. Fructus (siccus) 10–11 mm longus, 12–14 mm diametro, glabratus, laevis.

Shrub or small tree 2–3 m tall; stems initially very sparsely sericeous with hairs ca 0.5 mm long but soon quite glabrate. Lamina of larger leaves 14–21 cm long, 6.7–9.2 cm wide, elliptical or somewhat ovate, cuneate to almost rounded at base, very slightly revolute and reddish at margin, abruptly acuminate at apex to an attenuate tip 5–13 mm long, initially very sparsely sericeous but soon quite glabrate on both sides, bearing a pair of large impressed glands below at base and otherwise eglandular, the fine reticulum prominent on both sides, especially above; petiole 10–12 mm long, glabrous, eglandular; stipules 2–3 mm long, triangular, borne on adaxial face of petiole at base, glabrous. Inflorescence axillary, either simple or ternate with the 2 side branches axillary to much-reduced leaves (hardly larger than the floriferous bracts) at the first node, loosely sericeous to glabrescent, the individual pseudoracemes 3–6 cm long, the 8–14 flowers mostly decussate; floriferous bracts 1.5–2.5 mm long, triangular; peduncle 1–2.5 mm long; bracteoles ca 1 mm long, triangular, one or sometimes both bearing a large eccentric

abaxial gland, this becoming much enlarged and discoid in fruit; pedicel 3–4 mm long, to 8 mm in fruit. Sepals 1–1.5 mm long beyond glands, obtuse or rounded at apex, appressed, glabrous on both sides, often ciliate on margin, the anterior eglandular, the lateral 4 biglandular, the glands 2.5–3 mm long, elliptical or obovate, free and often reflexed distally. Petals yellow, glabrous, at least some glandular-fimbriate partly to completely around the limb; no flowers with a full set of petals available for description. Stamens glabrous; filaments 2–2.5 mm long, up to 1/2 connate, those opposite petals shorter and abaxially swollen at base; anthers 1–1.5 mm long, the connective yellow or light brown. Gynoecium bicarpellate; ovary 1.3 mm high, densely sericeous; styles 2, 1.4 mm long, quite distinct or connate only at base, glabrous except for base, the stigmas large, peltate. Fruit (dried) 10–11 mm long, 12–14 mm in diameter, depressed-globose, glabrate, the wall smooth.

Additional Specimens Examined. **Brazil**. Bahia: Mun. Itacaré, 2 km S of Itacaré at second beach, 14°17' S, 38°59' W, near sea level, forest on steep rocky hillside above beach, Apr fr, *Plowman et al. 10093* (K, MICH).

Bunchosia itacarensis is named for the only locality from which it is known. In this difficult genus it is always risky to speculate on relationships, but this species is presumably to be compared to *B. apiculata* Huber, which occurs in similar habitats from Ceará to French Guiana and also has a bicarpellate gynoecium with free styles. *B. apiculata* has a glabrous ovary, longer styles, much smaller leaves, simple inflorescences, shorter stipules, and smaller granulate fruits.

Bunchosia lindeniana Adr. Juss., Arch. Mus. Hist. Nat. 3: 335. 1843.—Type: Mexico. Veracruz: Miradores, *Linden 911* (lectotype, here designated: P-JU 11521!; isolectotypes: G, K!, MICH!).

Bunchosia lanceolata Turcz., Bull. Soc. Imp. Naturalistes Moscou 36: 582. 1863.—Type: Mexico. Veracruz: Orizaba, *Botteri s.n.* (KW?).

Bunchosia gentlei Lundell, Wrightia 6: 27. 1978.—Type: Guatemala. Dept. Izabal: Puerto Mendez, *Contreras 10323* (holotype: UTD, not seen; isotypes: BM!, K!, LL, MICH!).

This is probably the commonest species of *Bunchosia* in tropical Mexico and northern Central America, marked by its hairy three-carpellate ovary, emergent completely connate styles, strongly three-angled stigma, and glabrous or only sparsely sericeous leaves. It is extremely variable, especially in leaf size and shape, and the type of *B. gentlei* seems to be only a narrow-leaved form that does not merit taxonomic recognition. Of Jussieu's two syntypes, *Linden 911* is the better collection and I have chosen it as lectotype for that reason. Of the other syntype, *Galeotti 4340* from the same locality, I have seen the specimen in P, annotated by Jussieu, and two sheets in K; it represents the same species.

Niedenzu (1928, p. 653) recognized *B. lanceolata*, and he was followed by Standley & Steyermark (1946) in the Flora of Guatemala, but on the basis of Turczaninow's description alone I would be ready to assign his name to synonymy under *B. lindeniana*, which was not mentioned in the Flora of Guatemala. Niedenzu listed four Botteri collections from Orizaba: s.n. in 1856, 489 in 1857, 1093, and 1109. I have studied duplicates of 1093 and 1109 at K, and both are typical representatives of *B. lindeniana*, but I have not yet seen the specimen(s) available to Turczaninow, and until I can do that I prefer not to designate a lectotype for his name. Indeed, if he saw only one specimen, lectotypification will not be necessary.

Bunchosia ursana W. R. Anderson, sp. nov.—TYPE: COSTA RICA. Puntarenas: Golfito, Jiménez, entre Agua Buena y Banequitas, Jan fl, *Herrera 4806* (holotype: MICH!).

Frutex 1.5–3 m altus, ramis sparsim sericeis vel glabratis. Lamina foliorum majorum 17–26 cm longa, 7–10.5 cm lata, ovata vel elliptica, basi cuneata, apice acuminata acumine 13–25 mm longo, permox glabrata; petiolus 7–11 mm longus, sparsim sericeus vel glabratus; stipulae 0.4–0.7 mm longae. Sepala abaxialiter glabra vel proximaliter tomentosa distaliter glabra, margine ciliata, adaxialiter glabra. Petala glabra, 4 interiora limbo toto circuitu glanduloso-fimbriato; petalum posticum ungue 3.5–4.5 mm longo, limbo 3.5–4.5 mm longo latoque. Filamenta sepalis opposita longiora, petalis opposita breviora. Gynoecium tricarpellatum, glabrum, 4–4.5 mm longum, cylindricum; styli 3, basi connati, apice liberi, inter basim et apicem plus minusve cohaerentes; stigmata libera, magna, peltata.

Shrub 1.5–3 m tall; branches very sparsely sericeous to quite glabrate. Lamina of larger leaves 17–26 cm long, 7–10.5 cm wide, ovate or elliptical, cuneate at base, flat at margin or very slightly revolute, acuminate at apex to an attenuate tip 13–25 mm long, initially very sparsely sericeous but soon nearly or quite glabrate on both sides, bearing 1–2 glands below at base on each side of midrib and several in a distal row extending 1/3–2/3 of the lamina, usually closer to margin than midrib, the fine reticulum more or less prominent above; petiole 7–11 mm long, very sparsely sericeous to glabrate, eglandular; stipules 0.4–0.7 mm long, borne on adaxial face of petiole at base. Inflorescence an axillary pseudoraceme without vegetative leaves, white-sericeous to glabrescent in fruit, 6–17 cm long, the 15–35 (–50) flowers borne in no regular order; bracts 1–1.5 mm long, triangular; peduncle 0–0.7 (–1) mm long; bracteoles apical or subapical, 0.7–1 mm long, one of each pair usually bearing a large abaxial gland; pedicel 4.5–5.5 mm long. Sepals 1–2 mm long beyond glands, 1.5–2 mm wide, obtuse to rounded at apex, pressed against filaments in anthesis, abaxially glabrous or proximally tomentose and distally glabrous, ciliate on margin, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 2–3 mm long, glabrous or sparsely pilose, detached and spreading to reflexed in the distal 1/3–1/2. Petals yellow, glabrous, the inner 4 glandular-fimbriate all around limb, the outermost irregularly incised with some divisions glandular; 2 anterior-lateral petals strongly reflexed, with claw 1.5–2 mm long and limb 6–7 mm long and wide, deeply concave; posterior petal erect, with claw 3.5–4.5 mm long and limb 3.5–4.5 mm long and wide, flat, orbicular; 2 posterior-lateral petals intermediate in size, stance, and concavity of limb. Stamens glabrous; filaments 1.5–3.5 mm long, alternating between longer opposite sepals and shorter opposite petals, up to 1/2 connate; anthers 1.2–1.5 mm long, the connective yellow or light brown. Gynoecium tricarpellate, glabrous, 4–4.5 mm long, proximally cylindrical with the ovary (ca 1–1.5 mm high) grading imperceptibly into base of styles; styles 3, ca 3 mm long, connate at base, free at apex, strongly to weakly coherent between base and apex; stigmas free, large, peltate. Intact fruit not seen, but pyrenes ca 9 mm high and 7 mm across, suggesting a fruit at least 12 mm in diameter, probably larger.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica**. PUNTARENAS: steep forested slopes above Golfito, 8°38' N, 83°10' W, 100–300 m, Jan fl, *Burger & Matta 4718* (CR, F, MO, NY); moist forest on steep-sided ridge 5 km W of Rincón de Osa, Osa Peninsula, 8°42' N, 83°31' W, 50–200 m, Jan fl, *Burger & Liesner 7223* (CR, F); primary forest 2 km NW of Palmar Norte, 8°58'30" N, 83°28' W,

100–300 m, May fl, *Grayum et al. 7538* (MO); disturbed primary forest, Rincón de Osa, 20–300 m, Feb fl, *Liesner 1772* (MO), *1964* (MICH); Rincón de Osa, Oct fr, *Mata U. 473* (CR).

This species is known only from the Osa Peninsula of Costa Rica and adjacent areas on the mainland; the epithet reflects that provenance, *ursa* in Latin and *osa* in Spanish both meaning *she-bear*. *Bunchosia ursana* is distinguished from all other described species by its large nearly glabrous leaves, minute stipules, glandular-fimbriate petals, posterior petal with a very long claw, filaments alternating between long and short, glabrous tricarpellate gynoecium with the styles connate at base, coherent in middle, and free at apex, and three large peltate stigmas.

Bunchosia veluticarpa W. R. Anderson, sp. nov.—TYPE: COSTA RICA. Puntarenas: Monteverde lower community, Pacific slope, 10°18' N, 84°48' W, premontane wet forest, 1350 m, Aug fr, *Anderson 13805* (holotype: MICH!; isotypes: BM!, CAS!, CR!, DUKE!, F!, MEXU!, MO!, NY!). Fig. 1.

Arbor 4–18 m alta, ramis primo dense et pertinaciter aureosericeis. Lamina foliorum majorum 12–20.5 cm longa, 5.5–8.5 cm lata, supra primo aureosericea mox glabrata, subtus pertinaciter tomentosa. Inflorescentia 5–9 cm longa, sine foliis vegetativis. Petala flava, omnia eglandulosa vel petalum posticum basi limbi parum glandulosum, 4 interiora abaxialiter sparsim sericea. Antherae connectivo luteo vel brunneolo. Ovarium tricarpellatum, densissime tomentosum; stylus (ex 3 stylis connatis) tomentosus, stigmate trilobo. Fructus usque ad 3 cm longus, 2.5 cm diametro, dense et pertinaciter tomentosus.

Trees 4–18 m tall; stems densely and persistently golden-sericeous during the first year, glabrescent in later years. Lamina of larger leaves 12–20.5 cm long, 5.5–8.5 cm wide, elliptical or slightly obovate, cuneate at base, mostly acuminate (sometimes obtuse or acute) at apex, bearing several small impressed glands abaxially against base of midrib and many others scattered throughout lamina, initially loosely golden-sericeous above but soon glabrate except for midrib, densely and persistently tomentose below, the hairs of the midrib mostly golden and appressed, those of lamina white, with a relatively short stalk and a crosspiece 1–1.5 mm long, sinuous to twisted; petiole 8–12 mm long, loosely sericeous, eglandular or more commonly bearing a pair of impressed glands between middle and apex and a small bulbous gland at base near one or both stipules; stipules 1.5–2 mm long, borne on adaxial face of petiole at base, triangular, abaxially hairy, adaxially glabrous. Inflorescence an axillary pseudoraceme without vegetative leaves, golden-sericeous to subvelutinous, 5–9 cm long, the 9–24 flowers borne in no regular order; bracts 1–2.5 mm long, triangular; peduncle 1–3 mm long; bracteoles apical, 0.7–1.5 mm long, eglandular or more commonly 1 or both bearing a small abaxial gland; pedicel 4–5 mm long in flower, 7–8 mm long in fruit. Sepals ca 1 mm long beyond glands, rounded, densely tomentose abaxially except near margin, ciliate on margin, adaxially glabrous, appressed in anthesis, the glands 10, 2–3 mm long, free or some connate in pairs, glabrous. Petals yellow, all but the outermost very sparsely sericeous abaxially on claw and proximal midrib, the claw ca 1 mm long, the limb ca 2.5–4 mm long, largest and most deeply concave in outermost petal, all entire or erose but eglandular or the posterior with several slightly glandular thickenings near base of limb. Filaments 2.5–3 mm long, glabrous, ca 1/2 connate; anthers 0.8–1.5 mm long, glabrous, pressed against style in anthesis, the connective yellow or light brown, non-glandular. Ovary 1.5 mm

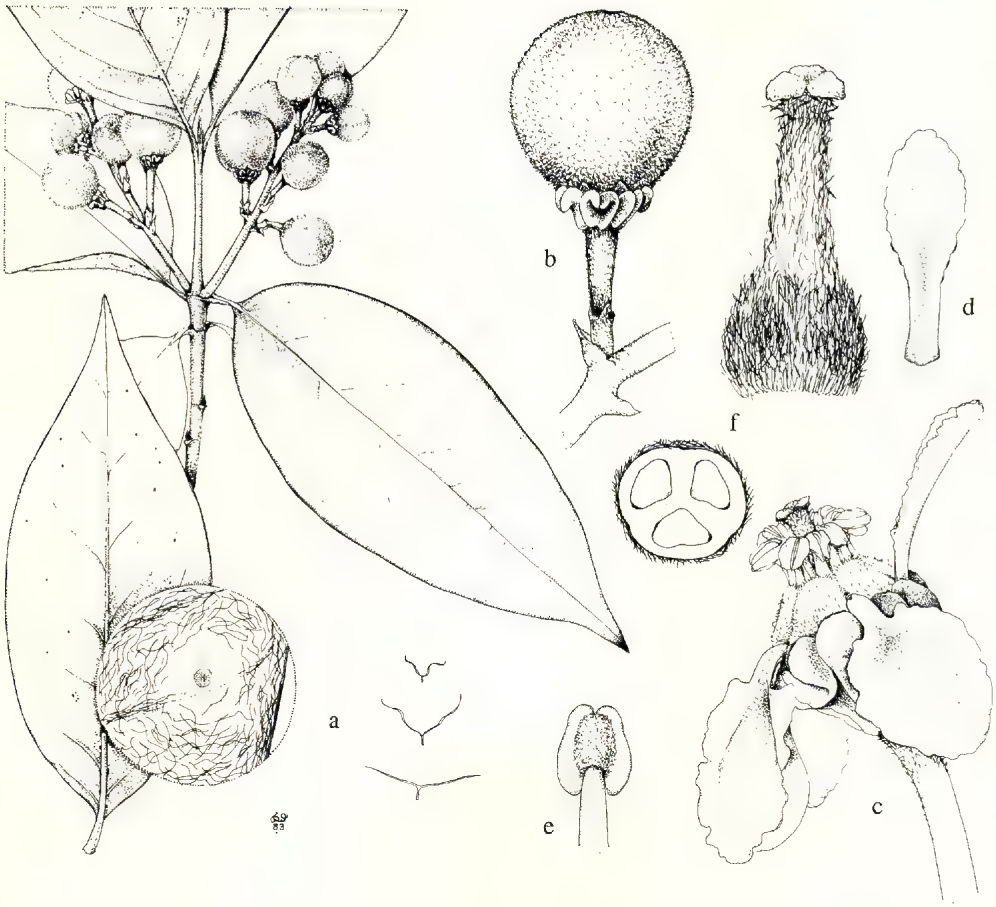

FIG. 1. *Bunchosia veluticarpa*. a) fruiting branch, ×0.5, with enlargement of detached leaf showing abaxial glands and vesture, ×5, and separate hairs, ×10; b) immature fruit, ×1.5; c) flower, side view, ×5; d) posterior petal, adaxial view, ×5; e) anther, abaxial view, ×10; f) whole gynoecium and cross-section of ovary, both ×10. Drawn by Karin Douthit, a–b from *Hartshorn 1904*, c–f from *Haber 303*.

high, depressed-globose, tricarpellate, very densely tomentose; style (formed by 3 completely connate) 2.5 mm long, tomentose its whole length, the stigma massive, 3-lobed. Immature fruit 15–25 mm long, 15–25 mm in diameter, green, orbicular to obovoid, at maturity (?) up to 30 mm long, turning yellowish, all sizes seen densely and peristently tomentose or subvelutinous with short twisted hairs, the vesture partially and unevenly abraded from some of the largest fruits, probably after collection.

Additional Specimens Examined. **Costa Rica**. Cartago: Moravia–La Chanchera, 1300 m, *León 1401* (US); 25 km SE of Turrialba between Jicotea and Moravia, wet secondary subtropical forest, 1000 m, Dec fl, *Little 20186* (CR).—Puntarenas: Monteverde, 1400–1500 m, Jul fr, *Dryer 1586* (F, MICH, MO), Mar fl, *Haber 303* (MICH), Jul fr, *Hartshorn 1904* (MICH, MO); Monteverde, 1300 m, pasture, Sep fr, *Haber ex Bello & Clagget 5532* (MICH); Monteverde to San Luis Valley, cliff edge along Río San Luis, 1000–1400 m, Jul fr, *Hammel 17092* (MICH).

Bunchosia veluticarpa is named for its densely and persistently hairy fruit, which is unlike anything I have seen in the tricarpellate species of the genus, in which the ovary is often hairy but the hairs soon fall from the enlarging fruit.

Other noteworthy characteristics are the sparsely sericeous petals and the many small glands scattered over the abaxial surface of the lamina. The tomentose leaves resemble those of *B. biocellata* Schlecht., which seems not to occur south of Nicaragua.

Burdachia prismatocarpa Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 330. 1840.—TYPE: BRAZIL. Amazônas: Rio Negro, Tefé ["Teffe"], *Martius* (lectotype, here designated: P-JU 11502!).

Jussieu had two syntypes, the Martius collection cited above and a specimen of *Poeppig 2911* from the same locality. Now that I have had the opportunity to study the specimens at Paris, I consider the best lectotype to be the Martius sheet in the Jussieu Herbarium; Jussieu received it as a gift from Martius in 1836.

Byrsonima altissima DC., Prodr. 1: 579. 1824. *Malpighia altissima* Aublet, Hist. Pl. Guiane 1: 455. 1775, not *M. altissima* Jacquin, 1764. *Byrsonima aubletii* Kostermans, Meded. Bot. Mus. Herb. Rijksuniv. Utrecht 25: 10. 1936.—TYPE: FRENCH GUIANA. "In sylvis Sinemariensibus," *Aublet* (holotype: BM!).

Byrsonima discolor Pilger, Repert. Spec. Nov. Regni Veg. 42: 179. 1937.—TYPE: BRAZIL. Pará: ilhas altas do Macujubinsinho, *Ducke s.n.* (holotype: RB 20950!).

In 1982 (p. 115) I described this rare plant under the name *Byrsonima aubletii* Kostermans, which was a mistake. De Candolle's combination based on Aublet's illegitimate name was inadmissible, but the epithet *altissima* was not preoccupied in *Byrsonima*, so I should have treated De Candolle's *B. altissima* as a new species dating from 1824. The New York Botanical Garden now has specimens of this species from Maranhão, and in those the leaves are substantially larger than in previous collections (lamina to 27 cm long and 13.5 cm wide, petiole to 50 mm long).

Byrsonima blanchetiana Miq., Linnaea 22: 799. 1850.—TYPE: BRAZIL. Bahia: Jacobine Moritiba, *Blanchet 3627* (holotype: U?; isotypes: BM!, K!, MO!, P!).

Niedenzu (1928, p. 752) recognized this species, placing it next to *Byrsonima correifolia* Adr. Juss., 1833. In synonymy under *B. blanchetiana* he placed the earlier name *B. bicorniculata* Adr. Juss., 1840, which he rejected on the basis of the fact that its name was based on an error of Jussieu's and did not accurately describe its anthers; that, of course, is not an acceptable basis for rejecting a name. Moreover, Niedenzu's key (p. 694) separates *B. blanchetiana* from *B. correifolia* on the basis of leaf shape, which is a difficult and variable character, and stipules supposedly distinct in *B. blanchetiana*, which is incorrect. Nevertheless, having now studied the types of all three species, I am maintaining *B. blanchetiana* as a good species. The most useful character distinguishing *B. blanchetiana* is the hairs on the abaxial surface of the lamina; they are sessile and have strongly twisted branches, producing a tightly tomentose vesture. In *B. correifolia* and *B. bicorniculata* the abaxial leaf hairs are long-stalked, with branches that are straight to somewhat twisted. Also, in *B. blanchetiana* the lamina is small, obovate, and tapered at the base, as noted by Niedenzu; its anthers are sericeous, with the connective much exceeding the locules and recurved at the apex. *Byrsonima blanchetiana* has been collected repeatedly in recent years in central Bahia, by R. Harley,

myself, and others. As for *B. correifolia* and *B. corniculata*, I remain undecided as to whether they both deserve to be recognized. There are differences between their types, but the two taxa are clearly closely related, and the more I see of the variation in their collections the more I doubt that they will both stand, but that problem needs more study.

Byrsonima concinna Bentham, London J. Bot. 7: 122. 1848.—TYPE: VENEZUELA ["BRITISH GUIANA"]. Bolívar: Roraima, *Robt. Schomburgk II 587/Rich. Schomburgk 912* (holotype: K! ["587 (912)"]; isotypes: BM! [587], CGE! [587 & 912, mounted together], F! [587], K! [912], NY! [912], P! [587], W [587]).

Byrsonima bracteolaris Bentham, London J. Bot. 7: 123. 1848.—TYPE: "BRITISH GUIANA." *Robt. Schomburgk* (holotype: K!).

I misapplied the name *Byrsonima bracteolaris* in my treatment of the Malpighiaceae of the Guayana Highland (1981, p. 109). Study of the type reveals it to lack vegetative vesture and to have the pedicel quite erect in fruit, so it has to be considered a specimen of *B. concinna* with hairy sepals. The two are listed here for the purpose of ensuring that the well-known epithet *concinna* is retained when the two simultaneously published names are considered synonyms. The species I treated under the name *B. bracteolaris* in 1981 is described below as *B. duidana*.

Byrsonima duidana W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Cerro Duida, summit, along valley forest between Central Camp and Brocchinia Hills, 1675 m, Aug fl, *Steyermark 58112* (holotype: NY!; isotype: VEN!).

Frutex vel arbor parva 2–4 m alta, ramis vegetativis sericeis mox vel demum glabratis. Lamina foliorum majorum elliptica vel obovata, 5.5–9 cm longa, 3–4.5 cm lata, apice obtusa vel rotundata, margine straminea, primo sparsim sericea mox glabrata, subtus non glauca; petiolus 8–12 (–15) mm longus; stipulae 2–3 mm longae, liberae, obtusae. Inflorescentia floribus singulis, bracteis bracteolisque 1.5–3.5 mm longis, 1.5–2.5 mm latis, triangularibus, post maturitate fructus persistentibus; pedicellus in fructu et floribus vetustioribus decurvatus. Sepala abaxialiter sericea vel tomentosa, adaxialiter glabra, per anthesin appressa, in fructu accrescentia. Petala alba demum rosea. Antherae 1.4–1.7 mm longae, glabrae, loculis 1.1–1.3 mm longis, dorsiventraliter complanatis, anguste alatis ala membranacea 0.1–0.2 mm lata, connectivo loculos 0.2–0.5 mm superanti. Ovarium glabrum; styli ca 3 mm longi. Fructus 5 mm diametro, 6 mm altus (siccus).

Shrubs or small trees 2–4 m tall; stems initially sericeous, soon or eventually glabrate. Lamina of larger leaves 5.5–9 cm long, 3–4.5 cm wide, elliptical or obovate, cuneate at base, obtuse or rounded and sometimes apiculate or retuse at apex, initially sparsely sericeous but soon quite glabrate, the margin yellow, 0.2–0.4 mm wide, revolute, not glaucous below, the lateral veins and reticulum usually prominent below or on both sides; petiole 8–12 (–15) mm long, loosely sericeous to glabrate; stipules 2–3 mm long, free, ovate, obtuse, abaxially sericeous to glabrate, adaxially glabrous except hirsute at base. Inflorescence 5–10 cm long, sericeous or tomentose, the flowers borne 1 per bract; bracts 1.5–3.5 mm long (the lowest pair up to 6 mm long), 1.5–2.5 mm wide, triangular, loosely sericeous to nearly glabrous, spreading or reflexed, persistent past maturity of the

fruit; peduncle none; bracteoles like bracts but usually smaller; pedicel 5–7 mm long, loosely sericeous or tomentose, circinate in bud, decurved in fruit and old flowers. Sepals all biglandular, 1.5 mm long beyond glands, ca 2 mm wide, rounded at apex, abaxially densely sericeous or appressed-tomentose, adaxially glabrous, appressed in anthesis, accrescent in fruit; glands 1.6–2 mm long, pink. Petals white, turning pink in age, glabrous, the outermost ± completely covering all others in bud. Filaments 2.6–2.8 mm long, abaxially glabrous, adaxially hirsute basally; anthers 1.4–1.7 mm long, glabrous, the locules 1.1–1.3 mm long, dorsiventrally flattened and bearing prominent membranous longitudinal wings 0.1–0.2 mm wide, the connective exceeding locules by 0.2–0.5 mm, the extension globose, glandular, inserted slightly between locules. Ovary ca 1 mm high, glabrous, all 3 locules fertile; styles ca 3 mm long, curved toward anterior sepal. Fruit 5 mm in diameter, 6 mm high (dried), ovoid, glabrous, subtended by the accrescent reddish calyx, the nut rugose.

Additional Specimens Examined. **Venezuela**. Amazonas: Cerro Sipapo, edge of savanna, Base Camp, 125 m, *Maguire & Politi 28287* (NY); Cerro Duida: forested and open area on plateau of Duida above Culebra, 3°36' N, 65°42' W, 1250 m, *Liesner & Morillo 18618* (MICH); Orinoco River, 30 km below La Urbana, 80 m, *Maguire & Maguire Jr. 29069* (NY); open scrub, Caño Negro basin, 2000–2300 m, *Maguire et al. 29679* (NY, VEN); summit, 1320–1440 m, *Tate 566, 595 & 740* (all NY); Cerro Marahuaca, forested steep sandstone southeast-facing slopes and bluffs, above branch of Caño Negro, south-central portion of meseta, downstream from "Sima Camp," 3°43' N, 65°31' W, 1220–1350 m, *Steyermark & Holst 130633* (MICH).

Collected with flowers in August and from January to March, and with fruits in November and March.

This is the species I treated under the name *Byrsonima bracteolaris* Bentham in 1981; see the discussion above under *B. concinna*. It is distinguished by its initially sericeous stems and leaves, the pedicels that are decurved in fruits and old flowers, the yellow margin of the lamina, and fact that the flowers are never more than one per bract.

Byrsonima macrophylla (Pers.) W. R. Anderson, comb. nov. *Malpighia macrophylla* Pers., Syn. Pl. 1: 506. 1805.—Type: Brazil. (holotype: P-JU 11485!).
Byrsonima nervosa DC., Prodr. 1: 579. 1824.—Type: Brazil. (holotype: G-DC, Field Mus. neg. 8024!).

This is a distinctive species of central Brazil, a shrub or small tree usually growing among rocks in the Serra do Espinhaço of Minas Gerais and Bahia. Its large leaves, rugose above and densely and persistently tomentose below, make it easy to recognize, even in a photograph. Persoon's type was not seen by De Candolle, who cited the Persoon name as a possible synonym. Jussieu received fragments of De Candolle's type from him, which are in a packet mounted on the P-JU sheet that bears Persoon's type, so Jussieu knew the two were the same species, but in his Monographie (1843, p. 287) he used De Candolle's name, presumably because it was the oldest name in the correct genus, and cited the Persoon name as a synonym. Niedenzu (1928, p. 742) was never able to see the specimens in Paris, so he cited the Persoon name as a possible synonym for *B. nervosa* DC., noting that if it really was the same species the correct name would have to be *B. macrophylla*. Having studied Persoon's type, I can attest to its identity, and therefore see no alternative to taking up his name in *Byrsonima*.

Byrsonima microphylla Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 334. 1840.—
TYPE: BRAZIL. Bahia: *Blanchet 48* (lectotype, here designated: P!; isolectotypes: BM!, P-JU!).

From Niedenzu's 1928 key and description in *Das Pflanzenreich* it is difficult to get much of a concept of this species. In fact it turns out to be quite distinctive and easily recognized, and it is of some ecological interest. Modern collectors have found it repeatedly in recent years in the Municipio de Salvador between the city of Salvador and the town of Itapuã some 30 km to the northeast along the coast, and I assume that Blanchet's three syntypes came from the same area. It grows in restinga vegetation on white sand dunes, especially near the Lagoa de Abaeté. The restingas from Salvador south are fairly well collected and I have not seen this species from elsewhere, which suggests that it may be a narrow endemic. If so, its continued existence may be threatened by development of the coast for tourist accommodations, although the nearness of its sand dunes to the airport may confer some protection. Some descriptive notes should make it easier for collectors and conservationists to recognize this attractive plant:

Shrub 1–2 (–3) m tall, the stems tomentose, eventually glabrescent. Lamina of larger leaves 1.7–4 cm long, 1.4–2.7 cm wide, elliptical or obovate to suborbicular, truncate or subcordate at base, slightly revolute at margin, broadly obtuse to rounded at apex, thinly tomentose to glabrate above, persistently moderately to densely tomentose below, the hairs medifixed and sessile with twisted arms, the midrib with an admixture of straight hairs; petiole 2–3 (–3.5) mm long; stipules 1.5–2 mm long, completely and smoothly connate, the pair broadly obtuse or rounded at apex. Inflorescence (2–) 3–6 cm long, bearing 6–12 (–16) flowers in the distal two-thirds; bracts 2.5–3.5 mm long, narrowly triangular, persistent to maturity of fruits or very belatedly deciduous; peduncle none or up to 2 mm long in the lowest flowers; bracteoles like bracts but smaller; pedicel somewhat circinate in bud, decurved in fruit. Sepals all biglandular, abaxially densely tomentose, adaxially glabrous, revolute at the apex and eventually on the sides. Petals initially white, turning red in age, the margin of the limb pilose with loose spreading hairs. Anthers glabrous, the locules cylindrical, the connective exceeded by locules. Ovary glabrous. Fruit (dried) ca 5 mm in diameter.

Relatively few species of *Byrsonima* combine white petals with anthers in which the connectives are shorter than or about as long as the locules, and only one such species other than *B. microphylla* occurs near the coast of Bahia. That is *B. cacaophila* W. R. Anderson, which is otherwise quite unlike *B. microphylla*. *Byrsonima cacaophila* is a tree 10–20 m tall that grows in the wet forests of cacao plantations. It has large leaves (lamina 13–24 cm × 5.5–10 cm, petiole 12–32 mm long), compound inflorescences with the cincinni bearing 1–3 flowers, sericeous anthers, and large fruits (11 mm × 15–18 mm dried).

The species that most resemble *B. microphylla* are shrubs that grow in rocky upland habitats of the Serra do Espinhaço of Bahia and Minas Gerais, e.g., *B. oxyphylla* Adr. Juss. and *B. variabilis* Adr. Juss. It seems likely that the ancestor of *B. microphylla* was adapted to the quartzitic sands of the Serra do Espinhaço and then managed to invade the sandy restingas. A parallel is to be found in *Peixotoa*, where *P. hispidula* Adr. Juss. is a restinga species in a genus of species that occur mostly in cerrado and campo rupestre; see the monograph by C. Anderson (1982).

Byrsonima rigida Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 334. 1840.—TYPE: BRAZIL. Mato Grosso: *Gaudichaud* (holotype: P!, Field Mus. neg. 35562).

Byrsonima gaultherioides Griseb. in Mart., Fl. Bras. 12(1): 112. 1858. *Byrsonima cornifolia* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Brauns-berg 1: 12. 1901, nom. superfl.—TYPE: BRAZIL. Goiás: Retiro, Rio "Uruhú" [Urubú?], *Pohl 1107* (lectotype, here designated: W, Field Mus. neg. 32417!).

This is a pretty pink-flowered shrub or subshrub with slender branches from a subterranean woody base, common in the cerrados of the Planalto of Brazil. Niedenzu (1928) recognized both *Byrsonima rigida* and *B. gaultherioides*. I can see tendencies toward differences, but no clear basis for recognizing two species. Plants from Mato Grosso (*B. rigida sensu stricto*) tend to be taller, stouter, and more branched, to spring from a stouter more erect rootstock, and to have shorter petioles and narrower leaves, whereas the plants from farther east (*B. gaultherioides*) tend to have shorter, slenderer, less-branched stems from a finer decumbent rootstock; their petioles are often longer and their leaves wider. There is overlap in all these characters, and until field studies permit evaluation of the habit and rootstock differences it seems best to treat these populations as a single species.

Niedenzu (1928) treated *Byrsonima rigida sens. lat.* and *B. triopterifolia* Adr. Juss. as the only members of his subseries *Eurylepis*. I agree that they are very similar and probably closely related, sharing these characteristics: leaves soon glabrate; stipules distinct; bracts and bracteoles persistent past maturity of the fruits; pedicels decurved in fruit; sepals glabrous on both sides; petals pink, sometimes fading to white; anthers glabrous, the locules cylindrical and not exceeded at the apex by the connective; ovary glabrous; fruits ca 5 mm in diameter (dried). The two can be distinguished by the characters in the following couplet:

1. Slender stems from a woody underground base, 0.2–1 (–1.5) m tall; lamina (1.5–) 2–3 (–4) times as long as wide, mostly elliptical or somewhat ovate; lateral veins and the coarser veinlets of the lamina prominent, but not the finest reticulum; red-clay cerrados of Minas Gerais, Goiás, the Distrito Federal, Mato Grosso, and Mato Grosso do Sul. *B. rigida.*
1. Woody, bushy shrubs 1–3 m tall; lamina 1–1.7 (–1.9) times as long as wide, elliptical or more commonly obovate to orbicular; intermediate veinlets and fine reticulum visible and ± prominent on both sides of the lamina, or at least abaxially; sandy soils among outcrops of quartzitic sandstone, Bahia. *B. triopterifolia.*

Camarea humifusa W. R. Anderson, sp. nov.—TYPE: BRAZIL. Goiás: Mun. Alto Paraiso, ca 20 km S of Alto Paraiso on highway GO-12, rocky campo at base of hill, 1100 m, Feb fl, *Anderson 11465* (holotype: MBM!; isotypes: MICH!, NY!). Fig. 2.

Herba perennis ramis procumbentibus e xylopodio turbinato radiantibus. Lamina foliorum majorum 12–26 mm longa, 3–7 mm lata, pilis omnibus medifixis; petiolus 0.5–1 mm longus. Flores omnes chasmogami, plerumque in umbellis terminalibus 2–4-floris portati; pedunculus 10–22 mm longus; pedicellus 3–5 mm longus. Petala aurantiaca, glabra, integra vel parum erosa; petalum posticum ungue 4–4.5 mm longo, limbo ca 5 mm longo, 7 mm lato. Filamenta 3.2–4 mm longa, glabra; antherae fertiles 0.7–0.8 mm longae, glabrae. Gynoecium glabrum; stylus ca 4.5 mm longus.

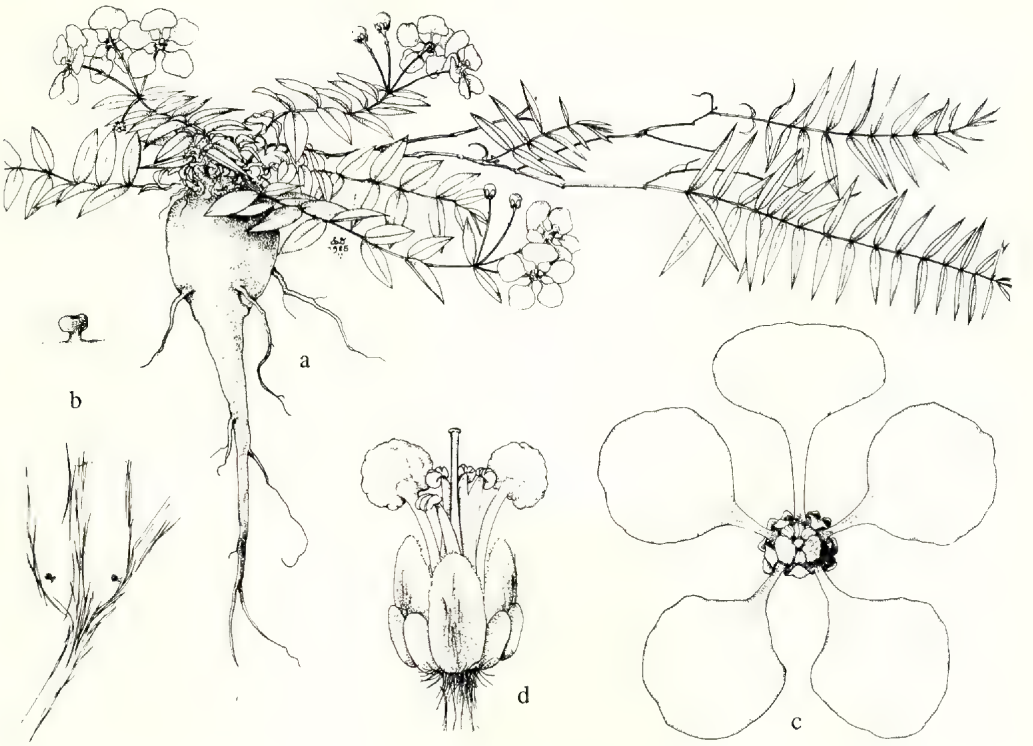

FIG. 2. *Camarea humifusa.* a) habit, ×0.5; b) base of leaf, abaxial view, ×5, and leaf gland, side view, ×25; c) flower, viewed from above with posterior petal uppermost, ×2.5; d) flower with petals removed, side view with anterior sepal in front, ×5. Drawn by Karin Douthit from *Anderson 11465.*

Perennial herb with strongly procumbent branches up to 25 cm long radiating from a flat-topped turbinate xylopodium up to 30 mm in diameter; stems wiry, up to 0.8 mm in diameter, initially subsericeous, glabrescent in age, the hairs fine, medifixed with arms of equal length, initially straight and more or less appressed but the arms often rising and becoming somewhat sinuous in age. Leaves strictly decussate; lamina of larger leaves 12–26 mm long, 3–7 mm wide, linear-lanceolate or narrowly ovate to ovate, cuneate to rounded at base, flat or very slightly revolute at margin, acute at apex, eglandular or biglandular below near base with 1 small peltate gland on each side of midrib borne on surface of lamina somewhat in from margin, densely sericeous on margins and abaxial midrib and thinly sericeous on adaxial surface and midrib, the hairs like stem hairs or V-shaped on the adaxial midrib, the older leaves sometimes glabrescent, the lateral veins obscure or invisible on both sides; petiole 0.5–1 mm long, sericeous; stipules ca 0.3 mm long, dark, subulate, borne on stem beside base of petiole. Flowers all chasmogamous, borne in a terminal umbel of (1–) 2–4 subtended by a pair of small vegetative leaves; floriferous bracts and bracteoles 1–1.5 mm long, narrowly triangular, the bracteoles borne at apex of peduncle; peduncle 10–22 mm long, pedicel 3–5 mm long, both sericeous or glabrescent like stems. Sepals 2.5–3 mm long, 1.3–1.7 mm wide, distinct, ovate or elliptical, rounded at apex, entire or slightly erose, abaxially sericeous in center and glabrous toward margin, sparsely ciliate on margin, adaxially glabrous, flat and appressed in anthesis, the anterior eglandular, the lateral 4 biglandular with the glands 1.3–1.5 mm long, elliptical. Petals orange-yellow, glabrous, entire or somewhat erose; lateral petals spreading, the claw 2–2.5

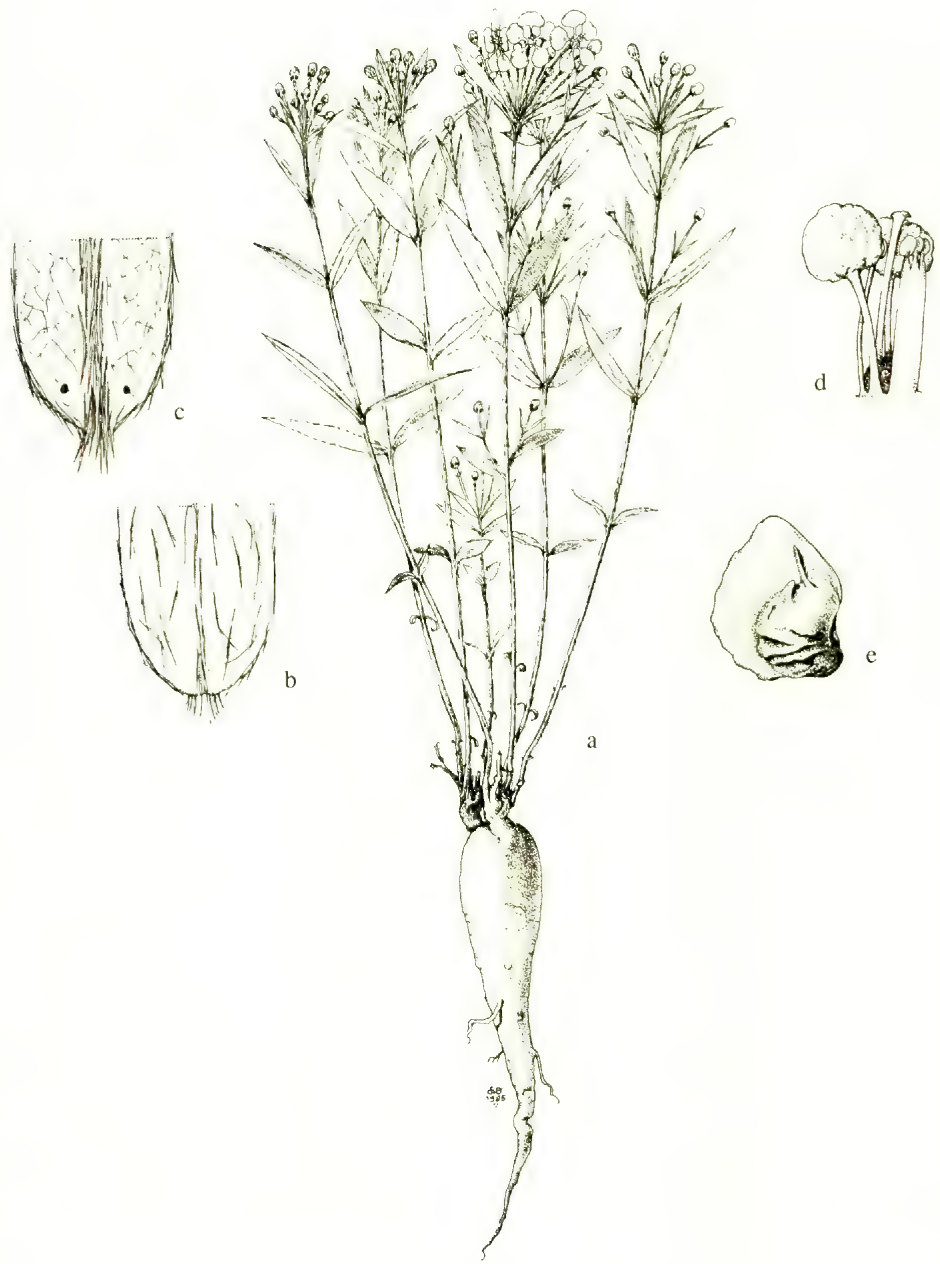

FIG. 3. *Camarea sericea*. a) habit, ×0.5; b) base of leaf, adaxial view, ×2.5; c) base of leaf, abaxial view, ×2.5; d) androecium and gynoecium, side view, the three stamens to right opposite the posterior petal and adjacent sepals, ×5; e) mericarp, side view, ×5. Drawn by Karin Douthit, a–d from *Pohl 1987* (W), e from *Glaziou 20747* (BR).

mm long, the limb 6–7 mm in diameter, obovate or nearly circular; posterior petal erect, the claw 4–4.5 mm long, the limb ca 5 mm long and 7 mm wide, oblate. Androecium glabrous, comprising 4 fertile stamens, opposite the posterior petal, posterior-lateral sepals, and anterior sepal, and 2 staminodes, opposite the anterior-lateral sepals; filaments straight, 3.2–4 mm long, shortest opposite the anterior sepal, the anterior 3 connate only at base, the posterior 3 connate for ca 2/3–4/5 of their length; fertile anthers 0.7–0.8 mm long; anthers of staminodes converted into

oblate lobed verrucose petaloid bodies 1.5–2 mm in diameter. Gynoecium glabrous; carpels 3, 1 anterior and 2 posterior, free but borne on a common torus, each bearing a dorsal crest and 1 lateral crest on each side; style 1, ca 4.5 mm long, straight, borne on inner face of anterior carpel, the stigma apical, capitate, elliptical. Fruit unknown.

This species is most like *Camarea sericea* St.-Hil., another species of the campos of Goiás. However, the strongly procumbent habit of *C. humifusa* sets it apart from *C. sericea*, and from other species of the genus. When more and better specimens are available, with ample flowers and fruits, it may well prove possible to find additional differences between *C. humifusa* and *C. sericea.* Compare Figure 2 (*C. humifusa*) to Figure 3 (*C. sericea*).

Clonodia complicata (H. B. K.) W. R. Anderson, Mem. New York Bot. Gard. 32: 206. 1981. *Hiraea complicata* H. B. K., Nov. Gen. Sp. 5 [quarto]: 171. 1822. *Mascagnia complicata* (H. B. K.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 4. 1908.—TYPE: VENEZUELA. Bolívar: Carichana, Orinoco, *Humboldt & Bonpland* (holotype: P-HBK!, Field Mus. neg. 37478).

Hiraea nitida H. B. K., Nov. Gen. Sp. 5 [quarto]: 171. 1822. *Mascagnia nitida* (H. B. K.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 4. 1908.—TYPE: VENEZUELA. Amazonas: S. Barbara del Alto Orinoco, *Humboldt & Bonpland* (holotype: P-HBK!, Field Mus. neg. 37479).

In my 1981 paper on the Malpighiaceae of the Guayana Highland, I speculated (pp. 206 and 209) that *Hiraea nitida* might represent an earlier name for *Clonodia racemosa* (Adr. Juss.) Nied., or a simultaneously published second name for *C. complicata*, or possibly some species not treated in my paper. Now that I have studied the types of both *H. complicata* and *H. nitida* I can report that they are indeed conspecific, and my purpose here is simply to place *H. nitida* formally in synonymy to ensure that the epithet *complicata* will continue in use for this species.

Echinopterys eglandulosa (Adr. Juss.) Small, N. Amer. Fl. 25: 148. 1910. *Bunchosia eglandulosa* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 325. 1840. *Echinopterys lappula* Adr. Juss., Arch. Mus. Hist. Nat. 3: 342. 1843, nom. superfl.—TYPE: MEXICO. Puebla: inter Acatlán & Chila, *Andrieux 498* (lectotype, here designated: P!, the sheet annotated by Jussieu; isolectotypes: K!, 2 sheets, both annotated by Jussieu; P-JU 11534!; P!, the sheet not annotated by Jussieu).

In my visits of the last ten years to P and K I have annotated as syntypes of this name their specimens of *Andrieux 498* and *Galeotti 4328*, even though Jussieu did not annotate the K sheets of *Galeotti 4328* and annotated the P sheet of *4328* only with his later, superfluous name, *Echinopterys lappula*. I was treating those two collections as syntypes of the 1840 name because both are cited in the 1843 Monographie. Jussieu cited no specimens in his 1840 Synopsis, so it is necessary to work from the Monographie when deciding what his types were, and because the two publications were only three years apart this practice is usually satisfactory. However, in this case it led me astray. I now realize that he had only *Andrieux 498* before 1840, which explains why only that specimen at P bears his annotations of both *Bunchosia eglandulosa* and *Echinopterys lappula*. Galeotti returned from

Mexico to Europe late in 1840, after the Synopsis was published, at which time he began arranging, numbering, and distributing his collections (McVaugh 1978). Paris must have received a sheet of *Galeotti 4328* sometime between 1840 and 1843, and that cannot be considered a syntype of Jussieu's 1840 name. There are now three sheets of *Andrieux 948* at Paris, two in the general herbarium and one in P-JU, but Jussieu's note in the Monographie, p. 342 ("v. s. herb. mus. Par.") indicates that he did not acquire his own sheet of *498* until later, and the fact that only one of the sheets in the general herbarium bears his annotation suggests that the second sheet may have been acquired later. Therefore, I am designating the annotated sheet of *Andrieux 498* in the general herbarium at Paris the lectotype of *Bunchosia eglandulosa*.

Malpighiaceae tribe **Gaudichaudieae** (Adr. Juss.) W. R. Anderson, stat. nov. Malpighiaceae subfamily Gaudichaudioideae ("Gaudichaudieae") Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 249. 1840.

Jussieu published this name with this spelling in 1840, but Morton (1968) argued that he was using it as the name of a subfamily whose spelling had to be corrected to Gaudichaudioideae. I think the argument might be made that Jussieu used the name in parallel with other names at the level of tribe, but I must admit that he also used it as a major subdivision of the family; it actually seems to have done double duty. While I would prefer to attribute the name of this tribe to Jussieu, I am validating it here at the level of tribe against the possibility that others will agree with Morton that the name has never been published, in spite of the fact that Jussieu's spelling is correct for a tribe under the present Code of Nomenclature.

Heteropterys alternifolia W. R. Anderson, sp. nov.—TYPE: BRAZIL. Bahia: Km 10–15 da BR 367 Porto Seguro para Eunapolis [39°10' W, 16°25' S], Oct fl, *Eupunino 330* (holotype: CEPEC!; isotype: MICH!). Fig. 4.

Liana lignosa, frutex, vel arbor usque ad 8 m alta, ramis sericeis. Folia alterna, subopposita, vel aliquando opposita; lamina foliorum majorum 6–10.3 cm longa, 2–4 cm lata, elliptica, basi cuneata, margine revoluta, apice obtusa vel rotundata saepe apiculata, supra permox glabrata, subtus pertinaciter metallosericea et aliquot glandulis parvis marginalibus munita; petiolus 4–13 mm longus, plerumque biglandulifer prope medium. Inflorescentia umbella (3–) 4–6-flora, pedunculo 3–6 mm longo, pedicello 5–7 mm longo. Petala lutea, glabra, carinata; petalum posticum limbo glandulosodentato proximaliter. Antherae 1–1.2 mm longae. Samara 35–50 mm longa, ala dorsali 30–42 mm longa, 12–20 mm lata, nuce 5–8 mm diametro, lateribus laevibus vel unicristatis crista brevi, usque ad 1.5 mm lata.

Woody vine, shrub to 4 m tall, or tree to 8 m tall; stems terete, sericeous to glabrate, bearing many small lenticels. Leaves alternate, subopposite, or sometimes opposite, varying on the same stem; lamina of larger leaves 6–10.3 cm long, 2–4 cm wide, elliptical or slightly ovate or obovate, cuneate at base, slightly to strongly revolute at margin, obtuse to rounded and often apiculate at apex, glabrous or very soon glabrate above, densely and persistently golden-, bronze-, or silvery-metallosericeous below with the hairs very short and tightly appressed, bearing a row of small glands below from base to apex, at or just within margin (these hidden when margin is revolute), the fine reticulum often prominent above;

FIG. 4. *Heteropterys alternifolia*. a) flowering branch, ×0.7, with enlargement of adaxial leaf surface, ×2; b) leaf base, abaxial view, ×3.5; c) umbel of flower buds, ×3.5; d) flower, anterior view, ×4.7; e) posterior petal, ×4.7; f) anthers, abaxial view (left) and adaxial view (right), ×17; g) stigma, ×27; h) samara, ×1.3. Drawn by Karin Douthit, a–g from *Eupunino 330*, h from *Harley et al. 17807*.

petiole 4–13 mm long, sericeous to glabrate, most often biglandular near middle but sometimes bearing 3–4 glands and occasionally eglandular; stipules not found. Inflorescence sericeous, an axillary or terminal umbel of (3–) 4–6 flowers, or a raceme of umbels, the stalk of the umbel 6–20 mm long; bracts and bracteoles persistent, eglandular, triangular or ovate, mostly appressed, abaxially sericeous, adaxially glabrous; bracts 0.8–1.2 (–2) mm long; peduncle and pedicel slender, 0.4–0.8 mm in diameter; peduncle 3–6 mm long; bracteoles 0.5–0.9 mm long, borne at or occasionally below apex of peduncle; pedicel 5–7 mm long (–10 mm in fruit), usually longer than peduncle. Sepals 1–2 mm long beyond glands, 1–1.4 mm wide, triangular, pressed against filaments in anthesis, abaxially sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular, the glands 1.8–3

mm long, elliptical, free at apex, the 2 glands adjacent to posterior petal sometimes long-decurrent. Petals yellow, glabrous, abaxially carinate, the lateral 4 reflexed, with claw 1–1.5 mm long and limb 3–4 mm long, 1.8–2.5 mm wide, denticulate; posterior petal erect to reflexed, with claw ca 2 mm long and limb 3–3.3 mm long, 2.2–2.7 mm wide, glandular-dentate on the proximal 1/2–2/3. Filaments 1.5–2 mm long, glabrous, 1/3–1/2 connate, straight or distally curved sideways or backwards; anthers 1–1.2 mm long, glabrous, alike, reflexed in anthesis. Ovary 1.5 mm high, sericeous; styles ca 1.3–1.5 mm long, glabrous, divergent, truncate or rounded dorsally at apex. Samara 35–50 mm long, sericeous, borne nearly erect; dorsal wing 30–42 mm long, 12–20 mm wide; nut subspheroidal, 5–8 mm in diameter, smooth-sided or bearing a single short lateral crest up to 1.5 mm wide.

Additional Specimens Examined: **Brazil**. Bahia: Mun. Maraú, BR-030, Km 11 Porto de Campinhos–Maraú, restinga, Feb fr, *Carvalho & Mattos Silva 213* (K, MICH); Mun. Salvador, dunas nos arredores da lagôa de Abaeté, May fr, *Carvalho et al. 692* (MICH, NY); 12 km S along road from Portal de Ilhéus just past Cururupe, 39°1' W, 14°54' S, disturbed restinga, sea level, Jan fr, *Harley et al. 17807* (MICH); Mun. Salvador, road from Itapuã to Aeroporto at intersection with Avenida Luis Viana Filho, 12°55' S, 39°21' W, relict area of high dunes, near sea level, Feb fr, *Plowman & Britto 13952* (F, MICH); Mun. Santa Cruz de Cabrália, 6–7 km de Santa Cruz de Cabrália na antiga estrada para a Estação Ecológica do Pau-Brasil, restinga arbustiva, Dec fl, *Sant'Ana 139* (MICH).

Heteropterys alternifolia belongs to series *Metallophyllis* Nied., a group of closely related species that is most diverse in eastern Brazil, especially near the coast. All the other species of the series have strictly decussate leaves. *Heteropterys coleoptera* Adr. Juss., which is known from restingas from Piauí to Rio Grande do Sul, is similar to *H. alternifolia* but differs in its opposite leaves, nonrevolute lamina, pedicels usually as long as or longer than the peduncles, shorter anthers, and well-developed lateral winglets on the smaller samara.

Heteropterys brachiata (L.) DC., Prodr. 1: 591. 1824. *Banisteria brachiata* L., Sp. Pl. 428. 1753.—Type: Herb. Cliffort. 169, *Banisteria* 2 (holotype: BM!).

Heteropterys tomentosa Hook. & Arn., Bot. Beechey Voy. 281. 1838, not *H. tomen-tosa* Adr. Juss. in St.-Hil., 1833. *Heteropterys beecheyana* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 278. 1840. *Banisteria beecheyana* (Adr. Juss.) C. B. Rob. in Small, N. Amer. Fl. 25: 134. 1910.—Type: Mexico. Guerrero: Acapulco (holotype: K!, annotated as *H. tomentosa* (by Hooker?) and as *H. beecheyana* by Adr. Juss.; photo MICH, WRA neg. 81-6-15).

Heteropterys retusa J. D. Smith, Bot. Gaz. (Crawfordsville) 16: 2. 1891. *Banisteria retusa* (J. D. Smith) C. B. Rob. in Small, N. Amer. Fl. 25: 136. 1910.—Type: Guatemala. Escuintla, *Smith 2068* (isotype: K!).

Banisteria simulans Small, N. Amer. Fl. 25: 136. 1910. *Heteropterys simulans* (Small) Nied. in Engler, Pflanzenr. IV. 141: 380. 1928.—Type: Mexico. San Luis Potosí: Los Caños, *Palmer 258* in 1902 (holotype: NY!; isotype: US!).

This species is extremely common, and correspondingly variable, throughout Mexico and south into South America. Niedenzu (1928) recognized both *H. beecheyana* and *H. brachiata*, assigning only four specimens from Venezuela to the latter. He was never able to study the type of Linnaeus's name, which I have now done. It clearly represents the species commonly called *Heteropterys beecheyana*, which must now be considered a synonym of *H. brachiata*. The following notes

were recorded for the Linnaean type: stems with many small lenticels; lamina roundish, rugose above, densely and persistently tomentose below with the veins and reticulum prominent; some leaves, especially the smaller ones, with 1–2 short-stalked peltate glands below at base of lamina; inflorescence a panicle of short few-flowered dense pseudoracemes or umbels; bracteoles borne at apex of peduncle; pedicel longer than peduncle; samara with several well-developed lateral winglets, not all parallel to the dorsal wing. The specimen is typical of the species as found in eastern Mexico, and may well have been collected by Houstoun in Veracruz.

Niedenzu (1928, p. 380) treated *Heteropterys simulans* under "Species incertae mihi invisae"; study of its type shows it to represent *H. brachiata*.

Heteropterys campestris Adr. Juss. in St.-Hil., Fl. Bras. Merid. 3: 33. 1833.—TYPE: BRAZIL. Minas Gerais: Tacaramby, Minas Novas, *Saint-Hilaire* Cat. B1 no. 1289 (lectotype, here designated: P!, the specimen labeled "TYPE," photo MICH, WRA neg. 81-25-18; isolectotypes: P!, photos MICH, WRA negs. 81-25-19 & 21).

Heteropterys discolor Adr. Juss. in St.-Hil., Fl. Bras. Merid. 3: 32. 1833.—TYPE: BRAZIL. Minas Gerais: Serra da Caraça, *Saint-Hilaire* (lectotype, here designated: P!, the specimen labeled "TYPE"; photos MICH, WRA negs. 81-26-3 & 4; isolectotypes: MICH!, P!).

Heteropterys confertiflora Adr. Juss. in St.-Hil., Fl. Bras. Merid. 3: 34. 1833.—TYPE: BRAZIL. Minas Gerais: Laranjeiras, S. João d'El Rey, *Saint-Hilaire* Cat. C1 no. 128 (lectotype, here designated: P!, the specimen labeled "TYPE," photos MICH, WRA negs. 81-25-32, 33 & 34; isolectotype: P!).

Heteropterys campestris is a shrubby species that is common and variable in the Planalto of central Brazil. Having studied their types, I see no basis for separating *H. discolor* from *H. campestris*. *Heteropterys confertiflora* is more difficult, being more divergent from *H. campestris* in its thinner lamina that is velutinous above and velutinous-tomentose below. However, there is no evidence that the plant was a vine and the petals are subequally carinate, none showing a really prominent winglet; those two characters indicate that this plant is probably not separable from *H. campestris*. Therefore I am treating *H. discolor* and *H. confertiflora* as synonyms. Niedenzu (1928) recognized both as good species, but he was never able to visit Paris and study the Saint-Hilaire collections there.

Heteropterys subhelicina Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 8: 60. 1926.—TYPE: BRAZIL. "Rio Branco" [=Roraima]: S. Marcos, *Ule 7808* (holotype: B†, Field Mus. neg. 12775; isotype: K!, photo MICH, WRA neg. 81-8-20).

Heteropterys catoptera W. R. Anderson, Mem. New York Bot. Gard. 32: 201. 1981.—TYPE: BRAZIL. Roraima: Caracaraí, *Pires et al. 14340* (holotype: IAN!; isotypes: MICH!, RB!).

Re-describing this species was an embarrassing mistake for which the only excuse I can offer is that I did not see an isotype of Niedenzu's name until after mine was published. In addition to the two types I have now seen several additional collections from Roraima (IAN, MICH) and several collections from the Rupununi of Guyana (K, MICH, US).

Hiraea bullata W. R. Anderson, sp. nov.—TYPE: BRAZIL. Bahia: Mun. Sta. Cruz de Cabrália, 4–6 km E of the Estação Ecológica do Pau-brasil (ca 17 km W of Porto Seguro), wet forest, Oct fl, *Mori et al. 10852* (holotype: CEPEC!; isotypes: K!, MICH!, NY!, RB).

Lamina foliorum majorum 5–8 cm longa, 3.5–6 cm lata, elliptica, basi rotundata, margine valde revoluta, apice late obtusa vel rotundata et mucronata, adaxialiter mox glabrata, abaxialiter pertinaciter velutina pilis T- et Y-formibus, coriacea, bullata costa et 5–7 nervis lateralibus supra profunde impressis et subtus prominentibus; petiolus 9–11 mm longus, stipulis 2–4 mm longis in dimidio distali instructus. Flores in umbellis 4-floris portati. Petala 4 lateralia lutea, eglandulosa; petalum posticum limbo rubro, margine toto circuitu glanduloso-dentato.

Woody vine, the stems tomentose-velutinous with an overstory of ± twisted T-shaped hairs and a longer-persisting understory of very short (ca 0.1 mm) Y-shaped hairs. Leaves decussate; lamina of larger leaves 5–8 cm long, 3.5–6 cm wide, elliptical or slightly ovate or obovate, rounded at base, strongly revolute at margin and eglandular or bearing a few small sessile glands near apex, broadly obtuse or rounded and mucronate at apex, soon glabrate above except subsericeous at base of midrib, densely and persistently hairy below with the midrib subsericeous and the rest velutinous with a mixture of long-stalked T- and Y-shaped hairs, coriaceous, the midrib and 5–7 pairs of lateral nerves, and to a lesser extent the scalariform tertiary veins, impressed above and prominent below, producing a bullate appearance; petiole 9–11 mm long, abaxially subsericeous and adaxially velutinous, bearing 2 protuberant glands at the apex or slightly beyond on the abaxial midrib; stipules 2–4 mm long, subulate, borne between middle and apex of petiole. Inflorescences axillary but most numerous distally to produce a terminal corymb, each inflorescence up to 3.5 cm long, single or 2 superposed in each axil, simple or ternate, the flowers borne in umbels of 4; bracts and bracteoles 0.7–1.7 mm long, triangular or ovate, abaxially sericeous; umbel without a glandular cushion between the bracteoles; pedicel 9–17 mm long, appressed-tomentose or subsericeous. Sepals ovate, obtuse or rounded at apex, appressed in anthesis, abaxially sericeous but distally glabrous, adaxially glabrous, the anterior eglandular, 2.5 mm long, 2 mm wide, the lateral 4 biglandular, 3 mm long, 2.5 mm wide, the glands 2–2.3 mm long. Petals glabrous, thick-textured, the lateral 4 yellow, spreading, erose or dentate but eglandular, with claw 1.5–2.5 mm long and limb 6–8 mm long and 6.5–8.5 mm wide, flat to concave, the posterior petal "red" (probably yellow in claw and red adaxially in limb), erect, glandular-dentate all around limb, with the thick claw 3–3.5 mm long and limb 5 mm long and wide, strongly concave. Filaments glabrous, connate at base, 2–3.5 mm long (longest opposite anterior sepal and shortest opposite posterior petal), straight or (especially opposite the lateral sepals) sigmoid; anthers 1–1.4 mm long, the connective dark red and yellow-glandular in the distal half. Ovary 1.4 mm high, densely dark-brown-hirsute; styles 3.5 mm long, glabrous or with a few hairs proximally, the anterior nearly straight and ± erect, the posterior 2 strongly arcuate toward posterior petal, acute or short-hooked at apex with the hook only 0.1–0.2 mm long. Fruit unknown.

Hiraea bullata is named for its leaves, in which the deeply impressed veins give the laminar tissue between them a raised, puckered appearance. It is these small, rounded, coriaceous, revolute leaves that distinguish this species from the other species with the leaves velutinous below, such as *H. ternifolia* (H. B. K.)

Adr. Juss. and *H. wiedeana* Adr. Juss. The red limb of the flag petal is also unusual in *Hiraea*. The species is known only from the type collection.

Hiraea christianeae W. R. Anderson, sp. nov.—TYPE: PERU. San Martín: San Martín, above Boca Toma del Shilcayo along Río Shilcayo N of Tarapoto, 06°30' S, 76°22' W, 400–450 m, tropical moist forest and gallery forest, May fr, *Knapp & Alcorn 7360* (holotype: MO!; isotype: MICH!).

Liana lignosa, ramis dense hirsutis pilis brunneis basifixis 4–6 mm longis patentissimis. Lamina foliorum majorum 14–21 cm longa, 8–11.5 cm lata, basi cordata, apice acuminata attenuataque, supra hirsuta, subtus velutina; petiolus 9–17 mm longus, hirsutus; stipulae ca 2 mm longae, infra medium petioli portatae. Umbella axillaris multiflora, in pedunculo hirsuto 1.5–2.5 cm longo elevata; pedicellus 15–20 mm longus, tomentosus. Styli arcuati apice dorsaliter apiculati. Samara alis lateralibus inter se liberis, 20–28 mm latis, 33–43 mm altis.

Woody vine; stems densely and persistently hirsute with stiff, dark brown, basifixed hairs 4–6 mm long spreading at 90°, many becoming broken or abraded on older stems. Lamina of larger leaves 14–21 cm long, 8–11.5 cm wide, somewhat obovate (i.e., widest above middle), cordate at base, acuminate at apex with an attenuate tip 5–17 mm long, bearing several small, short-peltate glands distributed evenly along the slightly revolute margin, densely and persistently hairy on both sides, the hairs of the adaxial surface basifixed, erect to inclined, mostly 3–4 mm long, like stem hairs but not as stout or dark, the abaxial margin with similar basifixed hairs, most of the abaxial surface velutinous with erect white T- or Y-shaped hairs, the abaxial midrib bearing a mixture of the two hair types, the principal lateral veins 8–10 on each side, interconnected by scalariform tertiary veins; petiole 9–17 mm long, densely hirsute like stems and with an underlayer of short white bifurcate hairs, biglandular between middle and apex with the small glands hidden among hairs; stipules ca 2 mm long, flattened-subulate, borne well above base of petiole but mostly below middle, hidden among hairs. Inflorescence an axillary umbel of many flowers (at least 10, probably 15–25 or perhaps more), raised on a hirsute stalk 1.5–2.5 cm long, the bracts and bracteoles 1–1.5 mm long, abaxially densely hirsute; pedicel (in fruit) 15–20 mm long, tomentose with mostly T-shaped hairs with short stalk and long crosspiece. Sepals abaxially densely hirsute, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular. Petals and stamens not seen. Styles (in fruit) strongly bowed and with a short but definite dorsal hook at apex. Samara hirsute on nut, hirsute to velutinous on wings with hairs mostly sub-basifixed and erect to inclined, the lateral wings distinct, flabellate, 20–28 mm wide, 33–43 mm high, sinuate or coarsely toothed; dorsal winglet 1–1.5 mm wide.

I am happy to name this most distinctive plant in honor of Christiane Anderson, astute student of *Stigmaphyllon*. The long spreading basifixed hairs of the stem and leaves are quite unlike anything I have seen in *Hiraea*, and indeed, most unusual for the family. The multiflowered umbels and curved apiculate styles place the species in section *Polyactinia* Nied. It is known only from the type, which bears mature fruits.

Hiraea haberi W. R. Anderson, sp. nov.—TYPE: COSTA RICA. Alajuela: Reserva Monteverde, Río Peñas Blancas, 10°20' N, 84°43' W, 820 m, Jun fl, *Haber 7247* (holotype: MO!).

Liana gracilis ramis usque ad 4 mm diametro. Lamina foliorum majorum 11–15.5 cm longa, 4.2–6 cm lata, adaxialiter mox glabrata, abaxialiter sericea pilis sessilibus vel subsessilibus, rectis, appressis. Umbella ca 20-flora, in pedunculo 8–22 mm longo, 0.5–3 mm sub umbella articulato, portata. Petala lateralia reflexa, subintegra vel denticulata; petalum posticum erectum, fimbriatum. Stylus anticus ± rectus et apice brevi-uncinatus; 2 styli postici arcuati et apice brevissime apiculati.

Woody vine, the stems sericeous, up to 4 mm in diameter, the epidermis split in age but not exfoliating in broad strips. Lamina of larger leaves 11–15.5 cm long, 4.2–6 cm wide, elliptical, chartaceous, cuneate to truncate at base, acuminate at apex, initially subsericeous but soon quite glabrate above, sericeous to eventually glabrescent below with the sessile or subsessile, ± straight, appressed hairs longest and most persistent on the midrib, eglandular or bearing a pair of small raised glands at base and 0–several small marginal glands, the 7–10 lateral veins prominent below and connected by very numerous strongly parallel scalariform crossveins; petiole 12–16 mm long, 1–1.5 mm in diameter, sericeous, eglandular or biglandular between middle and apex; stipules 0.5–1.6 mm long, subulate, borne on petiole 1.5–5 mm above base. Inflorescence axillary, an umbel of ca 20 flowers borne on a sericeous stalk 8–22 mm long, 0.7–1.2 mm in diameter, jointed 0.5–3 mm below umbel and bearing a pair of caducous much-reduced leaves or bracts at the joint; floriferous bracts and bracteoles 0.4–0.9 mm long, ovate, abaxially sericeous, adaxially glabrous, eglandular, persistent; pedicel 12–20 mm long, 0.7 mm in diameter, sericeous. Sepals 2–2.2 mm long, 1–1.6 mm wide, triangular, appressed in anthesis, abaxially sericeous, adaxially glabrous, all eglandular or the lateral 4 bearing 6–8 elliptical glands 0.9–1.6 mm long. Petals yellow, glabrous, thick-textured, the lateral strongly reflexed in anthesis, the claw 1.5 mm long and the limb ca 3 mm long, 3.5 mm wide, concave and revolute, denticulate or subentire; posterior petal erect, the claw 1.6–2.4 mm long, the limb 2.5–3 mm long and wide, flat, somewhat crumpled, long-fimbriate distally or all around the margin with the fimbriae often glandular-thickened distally. Filaments 2–2.8 mm long opposite sepals, 1.7–2.2 mm long opposite petals, glabrous, straight or sigmoid, connate at base; anthers 0.6–1.1 mm long, glabrous, the locules borne laterally on the dark red orbicular connective. Ovary 1 mm high, densely hirsute; styles glabrous, ca 2–2.3 mm long, the anterior ± straight and erect or leaning outward and bearing a dorsal hook ca 0.3 mm long at apex; 2 posterior styles strongly arcuate, bending from base toward posterior petal and then curving inward, dorsally apiculate at apex with the acute projection up to 0.1 mm long. Samara with lateral wings distinct at base and apex, trapezoidal, 20–22 mm wide, 27–32 mm high, sinuate or coarsely toothed, membranous, loosely sericeous with hairs spreading; dorsal wing ca 1.5 mm wide, ca 4.5 mm high, subentire or coarsely toothed; nut ca 4.5 mm in diameter, loosely sericeous.

Additional Specimens Examined. **Costa Rica.** Alajuela: Reserva Biológica Monteverde, Río Peñas Blancas, 10°20' N, 84°43' W, 800 m, Apr fl, *Haber 6983* (MICH); Upala, Colonia Libertad 2 km al NE de la Escuela, 300–400 m, May fr, *Herrera 1939* (MICH).—San José: Tarrazú, faldas del Cerro Nara, ca. Esquipulas, límite Quepos (Puntarenas) y Tarrazú, 9°29' N, 84°03' W, 350–400 m, Jul fr, *Gómez-Laurito 11583* (MO).

This species is named in honor of William Haber, whose tireless exploration of the forests in the vicinity of Monteverde has produced a rich harvest of botanical novelties. It belongs in section *Polyactinia* Nied., which is distinguished by having umbels of more than six flowers and curved styles that are dorsally apiculate at

the apex. Cuatrecasas (1958) treated four species in that section; I have compared *H. haberi* to the types of all those species, and it is clearly none of them. There seem to be at least three species of the section in Costa Rica, which can be separated by the following key.

1. Lamina velutinous below (except for midrib and lateral veins), the hairs stalked and Y- or T-shaped. *H. smilacina* Standley[1].
1. Lamina sericeous or subsericeous below, with most hairs sessile or subsessile and ± straight and appressed.
   2. Slender vine with stems up to 4 mm in diameter, the epidermis split in age but not exfoliating in broad strips; stipules up to 1.6 mm long; lamina up to 15.5 cm long and 6 cm wide; inflorescence stalk 8–22 mm long, jointed 0.5–3 mm below umbel. *H. haberi* W. R. Anderson.
   2. Stout liana with stems over 6 mm in diameter, the epidermis exfoliating in long, broad strips; stipules ca 4–7 mm long; lamina of larger leaves 15–45 cm long, 9–22 cm wide; inflorescence stalk 40–80 mm long, jointed 10–20 mm below umbel. *H. guapecita* Cuatrecasas.

Hiraea quapara (Aubl.) Sprague, J. Bot. 62: 22. 1924. *Banisteria quapara* Aubl., Hist. Pl. Guiane 1: 464, pl. 186. 1775. *Hiraea multiradiata* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 257. 1840, nom. superfl.—TYPE: FRENCH GUIANA. Aublet (lectotype, here designated: BM! (the three pieces with leaves and flowers but excluding the fruits), photos MICH, WRA negs. 81-2-25 & 26).

This is another species of Niedenzu's section *Polyactinia*. Jussieu rejected Aublet's name, probably because the type, which he had studied, included an admixture of three sapindaceous samaras, but that is not admissible under modern rules of nomenclature; it is, however, necessary to lectotypify Aublet's name so as to exclude the non-malpighiaceous element.

Field Mus. neg. 21341 shows two specimens of this species at C from the Vahl Herbarium, said to have come from von Rohr. In addition to pieces with leaves and flowers the photograph shows two loose sapindaceous samaras just like those with Aublet's type in BM. The coincidence is surely most unlikely, and raises the possibility that the specimen at C is a duplicate of the lectotype.

This name has been applied by recent authors (e.g., Niedenzu, 1928, and Cuatrecasas, 1958) both to plants of French Guiana and to a species of Colombia and Central America. This is understandable when only flowering material is studied, because leaves and flowers from the two areas are very similar. However, when one considers the fruits it immediately becomes evident that two different species are involved. The plants of Central America and Colombia, for which the oldest name appears to be *Hiraea smilacina* Standley, have fruits typical of the genus, with well-developed membranous flabellate lateral wings, producing a samara that looks like a butterfly. True *H. quapara* has weird fruits that are unique in the genus. The whole fruit is about 10–15 mm in diameter. The lateral wings are about 5 mm wide, thickened and corrugated, each with about 6 thick ribs on the lower side radiating from the nut. The dorsal wing is about 3 mm wide, rounded and thick, and extends almost the length of the nut. Between the lateral and the dorsal wings are a series of thick, irregular winglets and outgrowths

[1]Cuatrecasas (1958) called this *H. quapara* (Aubl.) Sprague, a separable species of the Guianas; see discussion under that name. *Hiraea smilacina* is a variable species that may yet yield to taxonomic subdivision.

oriented both parallel to the main wings and at right angles to them. The total effect is of a small, globose, burrlike fruit with much surface area, obviously adapted for dispersal by water, not by wind. *Hiraea quapara* has been collected twice in fruit, once in 1877 (*Mélinon 384*, P!) and again in 1976 (*Sastre 4692*, MICH!, P!).

Hiraea quapara is collected with some frequency in French Guiana, and in 1979 it was found for the first time in nearby Amapá, Brazil (*Austin et al. 7175*, MICH!, NY!). I have seen it from no other countries.

Lophopterys peruviana W. R. Anderson, sp. nov.—TYPE: PERU. Amazonas: Alrededor de yucui entsa 6 horas de pongo del Camino de Kusu, monte, 360–600 m, Mar fr, *Kayap 569* (holotype: MICH!; isotype: F!). Fig. 5.

Liana lignosa, ramis arcte sericeis pilis 0.1–0.3 mm longis. Lamina foliorum majorum 15–22.5 cm longa, 8.5–11 cm lata, elliptica, venis tertiariis scalariformibus; petiolus 16–21 mm longus, plerumque biglandulifer prope apicem. Bracteae bracteolaeque persistentes; bracteae 1.5–3 mm longae; pedunculus 0.5–2 mm long; bracteolae 0.8–1 mm longae; pedicellus 4–7 mm longus. Antherae 1.3–1.5 mm longae, inter loculos sparsim sericeae. Styli ca 1.5 mm longi, sericeae. Samara nuce 9–10 mm diametro, alis lateralibus 45–50 mm longis, 10–15 mm latis, ala dorsali 10–20 mm alta, 20–30 mm longa.

Woody vine climbing to 25 m; stems ridged, densely and persistently sericeous, the hairs only 0.1–0.3 mm long, so short and tightly appressed as to be not immediately evident. Leaves opposite or subopposite, or occasionally whorled (at least in the inflorescence); lamina of larger leaves 15–22.5 cm long, 8.5–11 cm wide, elliptical, rounded or cuneate at base, abruptly acuminate at apex, sericeous to very soon glabrate above, densely and persistently silvery-sericeous below with very short and tightly appressed hairs, eglandular or occasionally biglandular on margin at base, the 7–9 pairs of lateral veins connected by many very fine scalariform crossveins oriented at right angles to midrib, the reticulum prominulous above; petiole 16–21 mm long, persistently sericeous, usually bearing a pair of large glands near apex, sometimes bearing a second more proximal pair as well, occasionally apparently eglandular; stipules not found. Inflorescence densely and persistently golden- or brown-sericeous, paniculate, the flowers ultimately borne in pseudoracemes 6–12.5 cm long and containing 15–60 flowers; bracts and bracteoles persistent, the bracts 1.5–3 mm long, triangular, appressed or spreading at apex; peduncle 0.5–2 mm long; bracteoles like bracts but only 0.8–1 mm long; pedicel 4–7 mm long, 1.5 mm in diameter at apex, straight or curved upward in flower, sericeous like the inflorescence. Sepals ca 1 mm long beyond glands, broadly obtuse to rounded, abaxially densely sericeous to glabrescent, the anterior eglandular, the lateral 4 each bearing 1 very large circular gland 2–3.5 mm in diameter. Petals yellow, glabrous; open flowers with intact petals not seen; posterior petal ca 6 mm long, obovate, the limb long-decurrent on the claw, toothed with the proximal teeth glandular. Filaments 1.5–2 mm long, glabrous, up to 1/3 connate; anthers 1.3–1.5 mm long, sparsely sericeous between locules. Ovary 1 mm high, densely sericeous; styles ca 1.5 mm long, the anterior slightly shorter than the posterior 2, all divergent and sericeous their whole length. Samara with the nut spheroidal, 9–10 mm in diameter, sericeous or appressed-tomentose; lateral wings 45–50 mm long, 10–15 mm wide, linear or narrowly elliptical, sericeous; dorsal wing trapezoidal with the upper margin entire or slightly sinuous, 10–20 mm high,

FIG. 5. *Lophopterys peruviana*. a) fruiting branch, ×0.5; b) enlargement of adaxial surface of lamina to show scalariform crossveins, ×2.5; c) samaras, from below (left) and from the side (right), ×0.75; d) embryos, whole (right) and in longitudinal section (left), ×3; e) flower bud, ×5; f) flower, side view, lateral petals and 3 anthers removed, ×4; g) anther, abaxial view, ×15; h) gynoecium, anterior style in center, ×10; i) style tip, adaxial view, ×15. Drawn by Karin Douthit, a–d from *Kayap 569*, e–i from *Klug 654*.

20–30 mm long, sericeous. Seed globose, the embryo with one cotyledon longer and folded over the other distally.

Additional Specimens Examined: **Peru**. Loreto: Mishuyacu, near Iquitos, forest, 100 m, Dec fl, *Klug 654* (F, NY, US); Maynas, Iquitos, Km 44 carretera Iquitos–Nauta, bosque primario, 04°10' S, 73°20' W, 150 m, Dec fr, *Vásquez & Jaramillo 11420* (MICH).

This is one of two species of *Lophopterys* known from Peru; the other is *L. inpana* W. R. Anderson, which has been collected recently in the region of Pucallpa. *Lophopterys peruviana* is distinguished from *L. inpana* by its tighter stem vesture, mostly larger (especially wider) laminas with scalariform crossveins, larger petiole glands, shorter peduncles, small, more or less appressed bracts and bracteoles, sericeous anthers and styles, and larger fruits. The one flowering collection (*Klug 654*) differs from the other two collections in a number of details, and may represent a separable species, but such a determination will require better specimens than are available to me now.

Mascagnia chasei W. R. Anderson, sp. nov.—Type: Brazil. Bahia: Mun. Maracás, 8–18 km S of Maracás by old highway to Jequié, thicket, 900–1000 m, Feb fl, *dos Santos et al. 3480* (holotype: CEPEC!; isotypes: MICH!, NY!). Fig. 6.

Liana lignosa. Lamina foliorum majorum 3–7 cm longa, (1.2–) 1.5–3.5 cm lata, elliptica, supra mox glabrata, subtus pertinaciter sericea; petiolus 4–6 mm longus, eglandulosus. Pseudoracemus axillaris 1–3 cm longus, ex 4–10 floribus constans. Petala lutea, abaxialiter sericea, limbo toto circuitu fimbriato. Filamenta 1.3–2 mm longa, abaxialiter sericea; antherae 0.5–0.7 mm longae, glabrae. Styli 1.5 mm longi, apice dorsaliter brevi-apiculati. Samara alis lateralibus inter se liberis, 8–10 mm latis, 10–18 mm altis, crista dorsali nulla.

Woody vine with the slender stems initially sericeous, soon glabrate. Lamina of larger leaves 3–7 cm long, (1.2–) 1.5–3.5 cm wide, elliptical, cuneate at base, flat or slightly revolute at margin, mostly acute or slightly acuminate at apex (to obtuse or abruptly rounded), initially sericeous above but soon glabrate, densely and persistently sericeous below (very rarely irregularly glabrescent in age), bearing (0–) 1–3 small glands on proximal third of margin; petiole 4–6 mm long, sericeous to glabrate, eglandular; stipules ca 0.3 mm long, triangular, interpetiolar. Inflorescence an axillary pseudoraceme 1–3 cm long, shorter than the subtending leaf, sericeous throughout, comprising 4–10 mostly decussate flowers; bracts 0.7–1.5 mm long, narrowly triangular, appressed, eglandular; peduncle 0.7–2.5 mm long; bracteoles 0.5–0.8 mm long, triangular, appressed, eglandular, borne at apex of peduncle; pedicel 3.5–5 mm long. Sepals leaving the outer petal exposed during enlargement of bud, ca 2 mm long, appressed in anthesis, rounded at apex, abaxially densely sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands ca 1 mm long. Petals yellow, very densely golden-sericeous abaxially on claw and limb except near margin, fimbriate or glandular-fimbriate all around margin of limb, the claw 1.2–1.7 mm long, the limb 2.5–3.7 mm long, 2.3–3 mm wide, the lateral 4 reflexed and the posterior erect, the anterior-lateral pair with larger limbs than the posterior 3. Filaments 1.3–2 mm long, abaxially sericeous, adaxially glabrous, 1/4–1/2 connate; anthers 0.5–0.7 mm long, glabrous. Ovary sericeous; styles 1.5 mm long, subequal, sericeous at base, straight and erect to divergent, laterally flattened and dorsally short-apiculate at apex. Samara sericeous, with 2 discrete flabellate lateral wings, each wing 8–10 mm

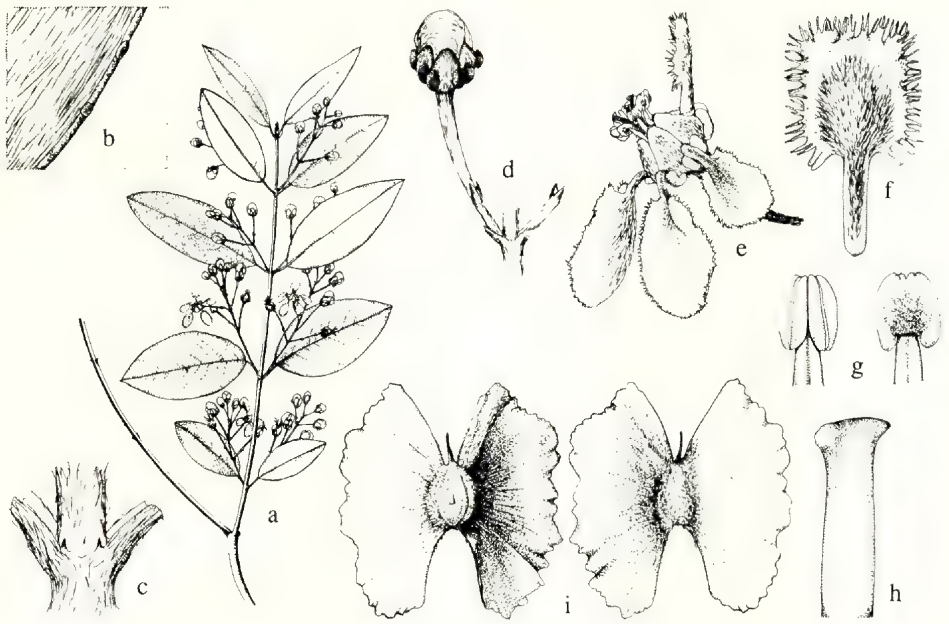

FIG. 6. *Mascagnia chasei*. a) flowering branch, ×0.5; b) leaf margin, abaxial view, ×10; c) node with stipules, ×5; d) flower bud, ×2.5; e) flower, ×3; f) posterior petal, abaxial view, ×6; g) anthers, adaxial view (left) and abaxial view (right), ×15; h) stigma, ×25; i) samaras, adaxial view (left) and abaxial view (right), ×2. Drawn by Karin Douthit, a–h from *dos Santos et al. 3480*, i from *Mori & King 12202*.

wide (measured from nut to farthest margin), 10–18 mm high (measured at right angles to width), erose or coarsely dentate; dorsal crest none.

Additional Specimens Examined. **Brazil**. Bahia: Sandy caatinga 21 km W of Breijão da Caatinga on road to Delfino, 600 m, Mar fl, *Anderson 11744* (K, MBM, MICH, NY); Mun. Andaraí, S of Andaraí on road to Mucugé, Serra do Sincorá, 480 m, Feb fl, *Anderson 13710* (MICH); Barreiras, Dec fl, *Black 54-17849* (IAN) & *54-17958* (IAN); Mun. Boninal, estrada Boninal–Piata Km 4, caatinga, 1100 m, Jul fr, *Coradin et al. 6546* (K); caatinga 9 km NE of Planalto along highway BR-116, 930 m, Mar fr, *Davidse et al. 11632* (MICH); 23 km E of Morro do Chapéu on road to Mundo Novo, 1000 m, Feb fr, *Irwin et al. 30734* (MICH, NY); Mun. Jequié, 4 km E of Jequié, caatinga, 600 m, Jul fr, *Mori & King 12202* (MICH, US).

Mascagnia chasei takes its epithet from Mark W. Chase, my collaborator in research on generic relationships in the Malpighiaceae. It is closely related to *M. chlorocarpa* (Adr. Juss.) Griseb.; the principal difference between them lies in their leaves, which are densely and persistently sericeous below in *M. chasei*, and soon quite glabrate in *M. chlorocarpa*. The leaves also tend to be longer and more attenuate at the apex in *M. chlorocarpa*. Most collections of *M. chlorocarpa* come from south and west of Bahia (Rio de Janeiro, Minas Gerais, São Paulo (not seen, cited by Niedenzu, 1928), Goiás, Paraguay, and Bolivia). However, I have seen one collection of *M. chlorocarpa* from Morro do Chapéu, Bahia (*Bautista 352*, K), very near the source of one of the paratypes cited above.

Mascagnia chlorocarpa (Adr. Juss.) Griseb. in Mart., Fl. Bras. 12(1): 93. 1858. *Hiraea chlorocarpa* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 259. 1840.—Type: Brazil. Rio de Janeiro: sylvis arenosis juxta Bertinga da Praia da Pedra, *Vauthier* (lectotype, here designated: P!, the specimen photographed

in Field Mus. neg. 35628; isolectotypes: G (the fruiting specimen in Field Mus. neg. 24286), K!, P!).

Heladena hassleriana Nied. in Chodat & Hassler, Bull. Herb. Boissier, Sér. 2, 7: 294. 1907.—TYPE: PARAGUAY. Río Apa, *Hassler 7837* (holotype: B†, Field Mus. neg. 12830; isotypes: BM!, K!, MICH!, MO!, P!)

Niedenzu maintained *Heladena hassleriana* in *Das Pflanzenreich* (1928), on the basis of the type, which was the only collection to which he ever ascribed that name. He knew it was unlike other species of *Heladena*, so he erected a section for it, which he called *Hassleria*. Study of *Hassler 7837* convinces me that it represents a flowering specimen of *Mascagnia chlorocarpa*, and in recent years the species has been collected in Paraguay with the diagnostic fruits (*Gentry et al. 59293*, MICH).

Mascagnia cordifolia (Adr. Juss. in St.-Hil.) Griseb. in Mart., Fl. Bras. 12(1): 95. 1858. *Hiraea cordifolia* Adr. Juss. in St.-Hil., Fl. Bras. Merid. 3: 19, pl. 164. 1833.—TYPE: BRAZIL. Near "Curumatahy," *St.-Hilaire* (lectotype, here designated: P!, the specimen annotated "TYPE," photos MICH, WRA negs. 81-21-17 & 18; isolectotypes: P!, 2 specimens, Field Mus. neg. 35629).

Mascagnia rubra Griseb. in Mart., Fl. Bras. 12(1): 90. 1858.—TYPE: BRAZIL. Goiás: near Natividade, *Gardner 3067* (isotype: K!).

Niedenzu (1928, p. 123) did not see the type of *M. rubra* and had to leave it under "Species incertae." It proves to be a synonym of *M. cordifolia*, a common and widespread species; noteworthy features of *Gardner 3067* that mark it as this species are: lamina velutinous on both sides; petiole biglandular at base; inflorescence elongate; some bracteoles bearing one large abaxial gland; petals distinctly alate.

Mascagnia divaricata (H. B. K.) Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 55. 1890. *Hiraea divaricata* H. B. K., Nov. Gen. Sp. 5 [quarto]: 169. 1822.—TYPE: VENEZUELA. Zulia: Dtto. Colón, entre Casigua El Cubo y km 8 de la vía rumbo a Palmira, Apr fl/fr, *Bunting 7371* (neotype, here designated: MICH!).

Hiraea oblongifolia DC., Prodr. 1: 585. 1824. *Mascagnia oblongifolia* (DC.) Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 55. 1890.—TYPE: COLOMBIA. Magdalena: Santa Marta, *Bertero* (holotype: G-DC; isotypes: MO!, P!).

Hiraea elegans Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 261. 1840. *Mascagnia elegans* (Adr. Juss.) Griseb. in Mart., Fl. Bras. 12(1): 95. 1858.—TYPE: PERU. Maynas: *Poeppig 2233* (lectotype, here designated: P!, the sheet photographed in Field Mus. neg. 35630; isolectotype: P!).

Hiraea pulcherrima Morong, Ann. New York Acad. Sci. 7: 67. 1892. *Mascagnia pulcherrima* (Morong) Skottsb., Kongl. Svenska Vetenskapsakad. Handl. 35(6): 4. 1901.—TYPE: PARAGUAY. Asunción, *Morong 626* (lectotype, here designated: MICH!; isolectotype: K!).

Mascagnia ixiamensis Rusby, Mem. New York Bot. Gard. 7: 271. 1927.—TYPE: BOLIVIA. Ixiamas, *Cárdenas 1999* (holotype: NY?; isotypes: K!, MICH!).

This is the species that has long been treated under the name *Mascagnia ovatifolia* (H. B. K.) Griseb., e.g., by Niedenzu, 1928, and Cuatrecasas, 1958. It is

widespread, occurring from Argentina to Nicaragua, and common throughout much of its range. As I explain below under *M. ovatifolia*, that name must be taken up for the plant long known as *M. nervosa*, and the oldest available epithet for this species is *divaricata*. The type of *Hiraea divaricata* was a collection made by Humboldt & Bonpland near Cumaná, Venezuela. The holotype is missing from P-HBK, and the isotype formerly at B (Field Mus. neg. 12694) no longer exists. As there appear to be no other isotypes, it seems necessary to designate a neotype. The collection I have chosen is from the lowlands of northern Venezuela and shows all of the characters that distinguish this species. The following couplet summarizes the diagnostic differences between *M. divaricata* and *M. ovatifolia*:

1. Dried lamina smooth above, the reticulum not raised and hardly visible; petiole usually bearing 2–4 glands near middle, sometimes eglandular; anthers pilose; samara usually about as high as wide, sometimes a little higher, sometimes a little wider. *M. divaricata.*
1. Dried lamina with the fine reticulum prominent above; petiole eglandular; anthers glabrous; samara usually distinctly wider than high. *M. ovatifolia.*

The smoothness of the lamina shows clearly in the photograph of the Berlin isotype of *H. divaricata*, and was also remarked by Kunth; in his protologues he described the lamina of *H. divaricata* as "obsolete reticulato-venosa" and that of *H. ovatifolia* as "reticulato-venoso." He also described the petioles of *H. divaricata* as "3–7-glandulosis" and those of *H. ovatifolia* as "eglandulosis," and he noted that the anthers of *H. divaricata* were "puberulae"; he did not see the anthers of *H. ovatifolia*.

Mascagnia lasiandra (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 5. 1912. *Hiraea lasiandra* Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 259. 1840.—TYPE: BRAZIL. "Martii Herb. Florae Bras." (holotype: P!).

Mascagnia nitens (S. Moore) Nied. in Engler, Pflanzenr. IV. 141: 123. 1928. *Hiraea nitens* S. Moore, Trans. Linn. Soc. London, Ser. 2, 4: 328. 1895.—TYPE: BRAZIL. Mato Grosso: *Moore 74* (holotype: BM!).

Niedenzu never saw Moore's type, so, although he could tell from the original description that *Hiraea nitens* belonged in *Mascagnia*, he had to place *M. nitens* under "Species incertae mihi non visae" in his 1928 monograph. Study of Moore's type in BM shows it to be conspecific with *M. lasiandra*; aside from general vegetative similarities, Moore's specimen shares with other collections of the species the characteristic short, dense, few-flowered raceme and the hairy filaments and sericeous anthers.

Mascagnia leonii W. R. Anderson, sp. nov.—TYPE: BRAZIL. Minas Gerais: Mun. Carangola, Fazenda Santa Rita, mata de encosta, 20°46' S, 42°02' W, 600 m, Aug fl, *Leoni s.n.* (holotype: GFJP 1213!; isotype: MICH!).

Liana lignosa. Lamina foliorum majorum 12–19 cm longa, 6–11.3 cm lata, mox glabrata; petiolus 15–30 mm longus; stipulae 3.5–6 mm longae, anguste triangulares vel subulatae. Bracteae 2–3.5 mm longae, eglandulosae; pedunculus 6–8 mm longus; bracteolae 1.2–1.7 mm longae, eglandulosae vel glandulam parvam gerentes; pedicellus 6.5–11 mm longus. Petala lutea, glabra, 4 lateralia abaxialiter carinata. Styli apice dorsaliter rotundati. Samara 21–26 mm alta, 19–25 mm lata,

ala laterali basi continua, apice paulo emarginata, crista dorsali 3–4 mm lata.

Woody vine; stems initially loosely appressed-tomentose, soon glabrescent. Lamina of larger leaves 12–19 cm long, 6–11.3 cm wide, ovate, rounded at base, reddish at margin, obtuse or abruptly acuminate at apex, initially appressed-tomentose above on midrib but soon glabrate, initially appressed-tomentose below on midrib and sparsely subsericeous on lamina with hairs ca 0.8 mm long but quite glabrate at maturity, bearing 0–3 impressed glands below near base on each side of midrib and 1–3 similar glands distally between midrib and margin, the lateral veins prominent below; petiole 15–30 mm long, tomentose to glabrate, eglandular; stipules 3.5–6 mm long, narrowly triangular or subulate, tomentose to glabrate, borne on stem beside petiole, persistent. Inflorescence an axillary panicle comprising dense pseudoracemes 2–5 cm long, borne singly or in pairs axillary to reduced leaves, each pseudoraceme containing 10–30 or more flowers; whole inflorescence tomentose or subsericeous, the pedicel glabrescent in fruit; bracts 2–3.5 mm long, narrowly lanceolate, eglandular; peduncle 6–8 mm long; bracteoles 1.2–1.7 mm long, eglandular or one or both bearing a small gland abaxially at base, borne at middle of peduncle or above but always well below apex; pedicel 6.5–9 mm long in flower, up to 11 mm long in fruit. Sepals appressed in anthesis, exceeding the glands by ca 1 mm, rounded at apex, abaxially loosely sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 2–2.5 mm long and slightly reflexed at apex. Petals yellow, glabrous, exposed during enlargement of the bud, the lateral 4 with the limb 4.5–5.5 mm long, ca 3 mm wide, oblong or almost rectangular, abaxially carinate or slightly winged, the claw 1–1.5 mm long; posterior petal with a smaller, not or hardly carinate limb and a thicker claw. Filaments 1.6–2.2 mm long, glabrous, nearly straight, connate only at very base; anthers 1.1–1.5 mm long, glabrous. Ovary densely appressed-hirsute; styles ca 2.5 mm long, subequal, divergent, especially the anterior, all 3 dorsally rounded at the apex. Samara 21–26 mm high, 19–25 mm wide, very broadly ovate to orbicular, very sparsely and loosely sericeous, the lateral wing membranous, continuous at base and apex, often shallowly notched at apex and slightly sinuate at margin; nut inserted slightly above center of wing; central dorsal winglet 3–4 mm wide; intermediate winglets none.

Additional Specimen Examined: **Brazil**. Minas Gerais: steep rocky lower slopes of Pico de Itacolomi, 3 km S of Ouro Preto, 1650 m, Feb fr, *Irwin et al. 29625* (MICH).

The epithet of this species honors Lucio de Souza Leoni, collector of the type and tireless curator of the Herbário "Guido Pabst" in Carangola, Minas Gerais. *Mascagnia leonii* is referable to the complex of *M. sepium* (Adr. Juss.) Griseb.; it is immediately separable from all other species in that complex by its extraordinarily long stipules, as well as by its large glabrate leaves, long peduncles, and carinate lateral petals. The type and paratype are somewhat different in their vesture, which is loose in the type, in their pseudoracemes, which are relatively short in the paratype, and in other details, but they share the large leaves and stipules. The whole complex needs thorough revision.

Mascagnia ovatifolia (H. B. K.) Griseb., Fl. Brit. W.I. 121. 1860. *Hiraea ovatifolia* H. B. K., Nov. Gen. Sp. 5 [quarto]: 170. 1822.—Type: Venezuela. Sucre: Cumaná, *Humboldt & Bonpland* (holotype: P-HBK!, photos MICH, WRA negs. 81-11-14, 15 & 16).

Mascagnia nervosa Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 12. 1908.—TYPE: COLOMBIA. Magdalena: Santa Marta, *H. H. Smith 344* (lectotype, here designated: US!; isolectotypes: MICH!, NY).

This species is a woody vine bearing pink or lilac flowers; it is common in the northern coastal states of Venezuela and also occurs in Trinidad, Colombia, and Panama. In the same area of northern Venezuela occurs a similar species with a much broader range; Humboldt and Bonpland collected them both near Cumaná. Recent students of the Malpighiaceae (e.g., Niedenzu, 1928, and Cuatrecasas, 1958) have called those two species *M. ovatifolia* and *M. nervosa*. When I studied the Humboldt & Bonpland collections at Paris in 1981, I found that the type of *Hiraea ovatifolia* actually represents the species that has been called *M. nervosa*, so the epithet *ovatifolia* has to go to that species and the former "*M. ovatifolia*" has to have another name, which is *M. divaricata*; for further discussion, see above under that name.

Cuatrecasas (1958, p. 367) lectotypified the name *Mascagnia nervosa* by citing as type the syntype *Otto 904* in B, but that specimen no longer exists, so it seems best to designate a new lectotype from among the duplicates of another syntype.

Mascagnia parvifolia (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 5. 1912. *Malpighia parvifolia* Adr. Juss., Arch. Mus. Hist. Nat. 3: 268. 1843.—TYPE: MEXICO. Oaxaca: *Galeotti 4327* (holotype: P!; isotypes: G, K!, P-JU!).

Mascagnia seleriana Loesener, Bull. Herb. Boissier 2: 543. 1894.—TYPE: MEXICO. Oaxaca: Mitla, *Seler & Seler 120* (holotype: B†, photo MICH!).

Hiraea parviflora Rose, Contr. U.S. Natl. Herb. 5: 139. 1897. *Mascagnia pringlei* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 9. 1908, nom. superfl.—TYPE: MEXICO. Puebla: Tehuacán, *Pringle 6274* (holotype of *parviflora*: US; holotype of *pringlei*: B†; isotypes: CM!, K!).

This is a common shrub on the dry calcareous hills of Oaxaca and southeastern Puebla. Most botanists have followed Small (1910) in calling it *Mascagnia seleriana*, and have ignored Jussieu's name, which Small did not mention. Niedenzu (1928) recognized both species, but he used the name *M. parvifolia* only for its type, and called the other collections he saw *M. seleriana*. It is true that Jussieu's type had unusually small leaves, but plants with leaves nearly or quite as small are to be found in any large assemblage of collections of the species, and I have no doubt that they represent a single taxon.

Mascagnia sericea Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 29. 1908. *Hiraea sericea* Engelm. in A. Gray, Pl. Wright. 1: 37. 1852, not *H. sericea* Adr. Juss., 1833. *Mascagnia cana* Small, N. Amer. Fl. 25: 120. 1910, nom. superfl.—TYPE: MEXICO. Durango: [La] Cadena, *Wizlizenus* (lectotype, designated by Small, 1910: MO).

Small (1910) rejected the combination *Mascagnia sericea* (Engelm.) Nied. because it was based on a later homonym, publishing instead as a *nomen novum* the name *Mascagnia cana*, and although Niedenzu (1928) retained the name *M. sericea*, most taxonomists have used Small's name for this species. However, there was no earlier *M. sericea*, so Small should have accepted Niedenzu's name as a

new species published in 1908, and the fact that he cited Niedenzu's name as a synonym makes Small's name superfluous. The correct name in *Mascagnia* is *M. sericea* Nied.

Engelmann cited two syntypes in the protologue, *Wizlizenus* from Cadena and *Gregg* from Mapimi; both localities are in eastern Durango near Gómez Palacios. The protologue of *M. cana* gave Cadena, Durango, as the type locality, which I take to be effective choice of the *Wizlizenus* specimen as the lectotype. The species is known from dry scrub on limestone soils in Chihuahua, Durango, Zacatecas, Coahuila, and San Luis Potosí.

Mezia huberi W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Depto. Atures, sandy savanna with rocks, in the region of hills and mountains S and SE of Cerro Camani, 20–25 km W of San Juan de Manapiare, 5°21' N, 66°15' W, 550 m, Oct fr, *Huber 4497* (holotype: MICH!; isotypes: MYF, NY!). Fig. 7.

Frutex vel arbor parva 2–8 m alta. Lamina foliorum majorum 9–17 cm longa, 5–10 cm lata, margine incrassata, subtus densissime et pertinaciter rufosericea. Bracteolae 7–9 mm longae, eglandulosae. Pedicellus 0.5–1 mm longus in flore, 2–5 mm longus in fructu. Petala lateralia abaxialiter sparsim tomentosa vel sericea; petalum posticum glabrum, limbo toto circuitu glanduloso-fimbriato vel distaliter dentato. Filamenta glabra, 2–2.7 mm longa, 1/3–2/3 connata; antherae glabrae. Styli recti, parum complanati, apice dorsaliter acuti vel truncati, anticus 2–2.5 mm longus, postici 2.5–3 mm longi. Samara 30–40 mm diametro; ala lateralis fere plana, sparsim tomentosa; 3 alae dorsales planae, parallelae; alulae transversales nullae.

Shrub or small tree 2–8 m tall, the stems densely and persistently sericeous, quadrangular becoming terete. Lamina of larger leaves 9–17 cm long, 5–10 cm wide, elliptical or somewhat obovate, truncate or cuneate at base, slightly revolute and notably thickened at margin, abruptly short-acuminate at apex with the acumen 5–9 mm long, initially sericeous above but soon glabrate except proximally on and near midrib, very densely and persistently sericeous below with the reddish or dark brown hairs sessile, straight, rather tightly appressed, completely concealing all tissues or the lateral veins glabrescent; lamina bearing below 1 large flat or sunken gland at base on each side of midrib and several small impressed glands distally in a single row several mm inside margin, the reticulum and 6–9 pairs of lateral veins raised on both sides but more below than above; petiole 10–15 mm long, persistently sericeous, eglandular; stipules reduced to minute triangular rudiments ca 0.2 mm high, borne on interpetiolar ridges and often hidden by stem hairs. Inflorescence sericeous to subvelutinous with short reddish or dark brown hairs, the finer axes flattened, containing persistent or deciduous much-reduced biglandular bracts subtending branches; floriferous bracts 4–5 mm long, obovate, concave, eglandular, abaxially densely sericeous, adaxially glabrous, deciduous during anthesis; peduncle 6–14 mm long in flower, 15–22 mm long in fruit, subvelutinous like the axes; bracteoles 7–9 mm long, eglandular, abaxially densely sericeous with the hairs reddish brown, adaxially glabrous or sparsely sericeous near margin; pedicel 0.5–1 mm long in flower, 2–5 mm long in fruit, hirsute with spreading basifixed or sub-basifixed hairs. Sepals 5–6 mm long beyond glands, 1.7–2 mm wide, revolute along sides, the glands 3–3.8 mm long, 1.3–1.7 mm wide, obovate or elliptical, compressed but distinct. Lateral petals with the claw 1.7–2 mm long, the limb 9–11 mm long and wide, orbicular, abaxially

FIG. 7. *Mezia huberi*. a) fruiting branch, ×0.5, with enlarged abaxial view of leaf base ×2.5; b) samara, ×1, abaxial view to left, side view looking into apical notch to right; c) umbel of flower buds with two cut off, ×2.5; d) open flower, side view, with one posterior-lateral petal removed, ×2.5; e) lateral petal, abaxial view, ×5; f) posterior petal, abaxial view, ×5; g) androecium laid out, adaxial view, the stamen opposite anterior sepal to left, ×5; h) anthers, side view, from opposite a sepal (left) and opposite a posterior-lateral petal (right), ×10; i) gynoecium, side view, anterior style to left, ×7.5. Drawn by Karin Douthit, a–b from *Huber 4497*, c–i from *Huber 449*.

sparsely tomentose or sericeous in proximal center, crumpled toward margin, erose; posterior petal with the claw 3.5–4 mm long, constricted at apex, the limb 5–7 mm long, 4.5–6 mm wide, suborbicular, glabrous, fimbriate all around the margin or only dentate at apex, the fimbriae rounded and slightly glandular-thickened distally. Filaments glabrous, 2–2.7 mm long, longest and stoutest opposite the 2 posterior-lateral petals, 1/3–2/3 connate; anthers all glabrous, 1.3–2 mm long, shortest opposite posterior petal, those opposite petals with locules equalling connective, those opposite sepals with locules exceeded by connective at apex by 0.3–0.9 mm. Styles straight and erect, stout, laterally somewhat flattened, proximally sericeous, acute or truncate dorsally at apex, the anterior style 2–2.5 mm long, the posterior styles 2.5–3 mm long. Samara subcircular, 30–40 mm in diameter, persistently tomentose or very loosely sericeous, densely so on nut and dorsal wings, more thinly so on lateral wing; nut with the ventral areole 6–7 mm high, 4 mm wide, ovate, bordered by 2 ribs that mostly persist on receptacle; lateral wing 15–18 mm wide, continuous at base, incised to nut at apex, membranous, nearly flat, entire at margin; central dorsal wing 4–5 mm wide, 7–11 mm high, semicircular, flat; 1 flat winglet 2–3 mm wide and 3–4 mm high present on each side of and parallel to central dorsal wing; otherwise intermediate ribs, crests, and winglets absent.

Additional Specimens Examined: **Venezuela**. Amazonas: Drainage of the Río Manapiare, gallery forest, savannas in mountains between Cerro Morrocoy to the south and the Serranía Colmena to the north, 5°20' N, 66°10' W, 200–350 m, Jan fl/fr, *Huber 449* (MICH, NY); Depto. Atures, drainage of the Río Manapiare, savannas at the foot of the mountains N of Cerro Morrocoy, near "Pozo de la Carlina," ± 12 km W of San Juan de Manapiare, 5°19' N, 66°6' W, 150 m, Oct fl/fr, *Huber 1191* (MICH).

I first saw a specimen of this species while my 1981 paper on the Malpighiaceae of the Guayana Highland was in press, and in a footnote (p. 236) I referred it (with some reservations) to *Mezia rufa* W. R. Anderson. As more collections of both species have accumulated I have come to realize that this plant from near San Juan de Manapiare is a distinct endemic species, and I am glad to name it for its collector, Dr. Otto Huber, the excellent botanist who has made such a fine contribution to our knowledge of southern Venezuela in the last 15 years. The following couplet compares *Mezia huberi* to *Mezia rufa*.

1. Habit a shrub or small tree 2–8 m tall; lamina of larger leaves 9–17 cm long, 5–10 cm wide; bracteoles 7–9 mm long; samara 30–40 mm in diameter, the central dorsal wing and 2 parallel winglets flat, the latter not connected by transverse winglets to the lateral wing; lateral wing of samara nearly flat, tomentose, the hairs sinuous and spreading. *M. huberi.*
1. Habit a woody vine; lamina of larger leaves 16–28 cm long, 10–17 cm wide; bracteoles 10–12 mm long; samara 60–70 mm in diameter, the central dorsal wing and 2 parallel winglets strongly corrugated and each of the latter connected to the lateral wing by several corrugated transverse winglets; lateral wing of samara wrinkled or corrugated, sericeous, the hairs straight and tightly appressed. *M. rufa.*

Pterandra egleri W. R. Anderson, sp. nov.—Type: Brazil. Pará: Alto Tapajós, Rio Cururú, Erereri, Jul fl, *Egler 1033* (holotype: MG 23.712!; isotypes: HB!, IAN!, MICH!, NY!).

Frutex 0.5–1.5 m altus. Lamina foliorum majorum 5.5–9 cm longa, 2.3–4.3 cm lata, ovata vel elliptica, subtus pertinaciter tomentosa pilis brunneis, brevistipitatis, usque ad 1.2 mm longis, serpentinis. Fasciculi florum 5–10-flori; pedicelli 11–15

mm longi. Petala alba, limbo 3.5–4 mm longo, 3.2–3.7 mm lato, rotundato vel late obovato. Antherae 1–1.4 mm longae, persistentes, alis 0.2–0.4 mm latis, connectivo apice rotundato.

Low spreading shrubs 0.5–1.5 m tall; branchlets persistently sericeous. Lamina of larger leaves 5.5–9 cm long, 2.3–4.3 cm wide, ovate to elliptical, cuneate to rounded at base, mostly acute or obtuse (sometimes slightly acuminate) at apex, containing many angular translucent dots in the adaxial epidermis at and just within the margin (these especially visible in young leaves), appressed-tomentose to eventually glabrate above, densely and persistently tomentose below or the oldest leaves belatedly and patchily glabrescent, the hairs light brown, short-stalked, up to 1.2 mm long, serpentine to somewhat twisted, strongly non-parallel so as to produce a tomentose rather than a sericeous effect, the midrib and 6–8 pairs of lateral veins obscure above and prominent below, the tertiary veins scalariform and often prominulous below; petiole 6–10 mm long, persistently sericeous; stipules 3–4.5 mm long, completely and smoothly connate, obtuse or rounded at apex, abaxially sericeous or eventually glabrescent, adaxially tomentose. Flowers borne in fascicles of 5–10 axillary to (or somewhat above) the scars of fallen leaves (or bracts?); floriferous bracts and bracteoles similar, 0.7–1.3 mm long, 0.3–0.8 mm wide, triangular or linear, abaxially sparsely sericeous, deciduous in fruit; pedicel 11–15 mm long, 0.5–0.7 mm in diameter, sericeous. Sepals 1.5–2.2 mm long beyond the glands, 1.5–1.8 mm wide, triangular, rounded or obtuse at apex, revolute in anthesis, abaxially sericeous, adaxially glabrous, all biglandular, the glands 0.9–1.2 mm long, flat, elliptical. Petals white, abaxially densely tomentose-sericeous on claw and much of limb but glabrous in the marginal 0.5 mm, adaxially glabrous, the claw 1–1.3 mm long, the limb 3.5–4 mm long, 3.2–3.7 mm wide, round or broadly obovate, erose, the posterior petal slightly larger than the lateral 4. Filaments 1.5–2.8 mm long; anthers 1–1.4 mm long, persistent in fruit, the wings dark red, 0.2–0.4 mm wide, widest at base, slightly shorter than locules, the connective not enlarged, or red and slightly swollen at apex. Ovary with carpels ca 1 mm high, appressed-tomentose; styles slightly subapical, 3.5–5 mm long. Immature cocci ca 3 mm high, spheroid with a base of spongy tissue, densely tomentose.

Additional Specimens Examined: **Brazil**. Pará: Alto Tapajós, region of Missão Velha, a Mundurukú village ca 2 km N of Rio Cururú, 7°45' S, 57°20' W, 200 m, upper drier part of sandy floodplain between river and village, with scattered shrubs and small trees, partly inundated with runoff water at this season, Feb fl/imm fr, *Anderson 10895* (IAN, MICH, NY).

This species is named in honor of Walter A. Egler, the Brazilian botanist who collected the type and many other Amazonian plants before his tragic death on a field trip in Amapá in 1961. It is probably closest to *Pterandra evansii* Cuatr., but the latter differs in a number of characters, of which the most easily observed are these: leaves sericeous below, the hairs sessile, straight, parallel, up to 0.5 mm long; flowers borne in fascicles of 2–5; pedicels 14–21 mm long; petals narrowly obovate.

The fascicles of flowers in this species are borne at several nodes between vegetative leaves of the previous year and of the current year. I have some reason to believe that the scars subtending those fascicles are from bracts like those described below for *P. hatschbachii*, but the evidence for that is not satisfactory in the specimens now available; younger stems collected while the flowers are in bud and the subtending leaves or bracts are still present will resolve the question.

Pterandra hatschbachii W. R. Anderson, sp. nov.—TYPE: BRAZIL. Mato Grosso: Mun. Alto Araguaia, Rib. Claro, campo rochoso, Sep fl, *Hatschbach 35085* (holotype: MBM 31636!; isotype: MICH!). Fig. 8.

Suffrutex ramo crassiore subterraneo decumbenti et ramis erectis 5–25 cm altis, usque ad 2.5 mm diametro, sericeis. Lamina foliorum majorum 6–12.5 cm longa, 2.3–4.4 cm lata, plerumque obovata, basi bullata; petiolus 1–2 (–2.5) mm longus; stipulae 1–2 mm longae, liberae vel connatae. Fasciculi florum (4–) 5–9-flori; pedicellus 11–25 mm longus. Petala rosea, limbo 5–7.5 mm longo, 4–7.5 mm lato, rotundato vel late obovato. Antherae 1.2–1.9 mm longae, deciduae, alis 0.1–0.2 mm latis, connectivo apice triangulari.

Shrublet with woody underground stems trailing and rooting, the erect aboveground stems forming dense carpets in grassy campos, 5–25 cm tall, not or hardly branched, wiry (up to 2.5 mm in diameter), initially densely sericeous, eventually glabrate. Lamina of larger leaves 6–12.5 cm long, 2.3–4.4 cm wide, obovate to nearly elliptical but usually widest at least somewhat above middle, cuneate to rounded at base, thickened and often slightly revolute at margin, obtuse to broadly rounded and often apiculate at apex, often showing many angular translucent dots scattered throughout adaxial epidermis and near margin in abaxial epidermis, bullate at base, initially sericeous on margin, midrib above and below, and lateral veins below, and with scattered more or less appressed hairs on laminar tissue, mostly soon glabrate or persistently sericeous on midrib below, the midrib and 5–7 pairs of lateral veins flat above and raised below, the reticulum white and visible outlining dark areoles, especially below; petiole 1–2 (–2.5) mm long, persistently sericeous or eventually glabrate; stipules 1–2 mm long, distinct or completely connate (with both conditions on the same stem!), narrowly triangular when distinct, the pair broadly triangular when connate, abaxially sericeous to glabrate, adaxially hirsute. Flowers borne in fascicles of (4–) 5–9 axillary to sericeous triangular bracts 2–2.5 mm long and 2 mm wide, or the scars where they were produced, between previous year's vegetative leaves and the flush of new leaves; floriferous bracts and bracteoles 0.7–1.5 mm long, 0.3–0.7 mm wide, narrowly to broadly triangular, sparsely pilose or glabrous, persistent; pedicel 11–25 mm long, 0.4–0.5 mm in diameter, loosely white-sericeous. Sepals 2–3 mm long beyond glands, 1.8–2.3 mm wide, triangular or ovate, obtuse or rounded at apex, revolute at apex and often at sides, abaxially sericeous, adaxially glabrous, often with translucent dots in the adaxial surface, all biglandular, the glands 0.9–1.5 mm long, flat, elliptical or obovate. Petals pink, turning white in age, abaxially sericeous only on claw and/or on midrib to center of limb, adaxially glabrous, usually showing glandular dots in the center abaxially, the claw 0.5–1.5 mm long, the limb 5–7.5 mm long, 4–7.5 mm wide, round or broadly obovate, erose, the posterior petal somewhat larger than the lateral 4 and with a thicker claw. Filaments 1.7–3 mm long; anthers 1.2–1.9 mm long, deciduous in fruit, the wings 0.1–0.2 mm wide, widest at base and extending upward only 3/4 of the locule, the connective darkening in age, with a triangular apical extension 0.1–0.2 mm long. Ovary with 3 (–4) carpels ca 1 mm high, densely hirsute; styles slightly subapical, 3–5 mm long. Immature cocci ca 3.5 mm high, spheroid, pubescent with soft white basifixed hairs.

ADDITIONAL SPECIMENS EXAMINED. **Brazil**. MATO GROSSO: Mun. Alto Araguaia, vicinity of Riberão Claro, NW of Alto Araguaia, grassy campos, 800 m, Feb fl, *Anderson 11400* (MICH); Alto Araguaia, arredores, campo arenoso, Nov fl/imm fr, *Hatschbach 33276* (MBM, NY).

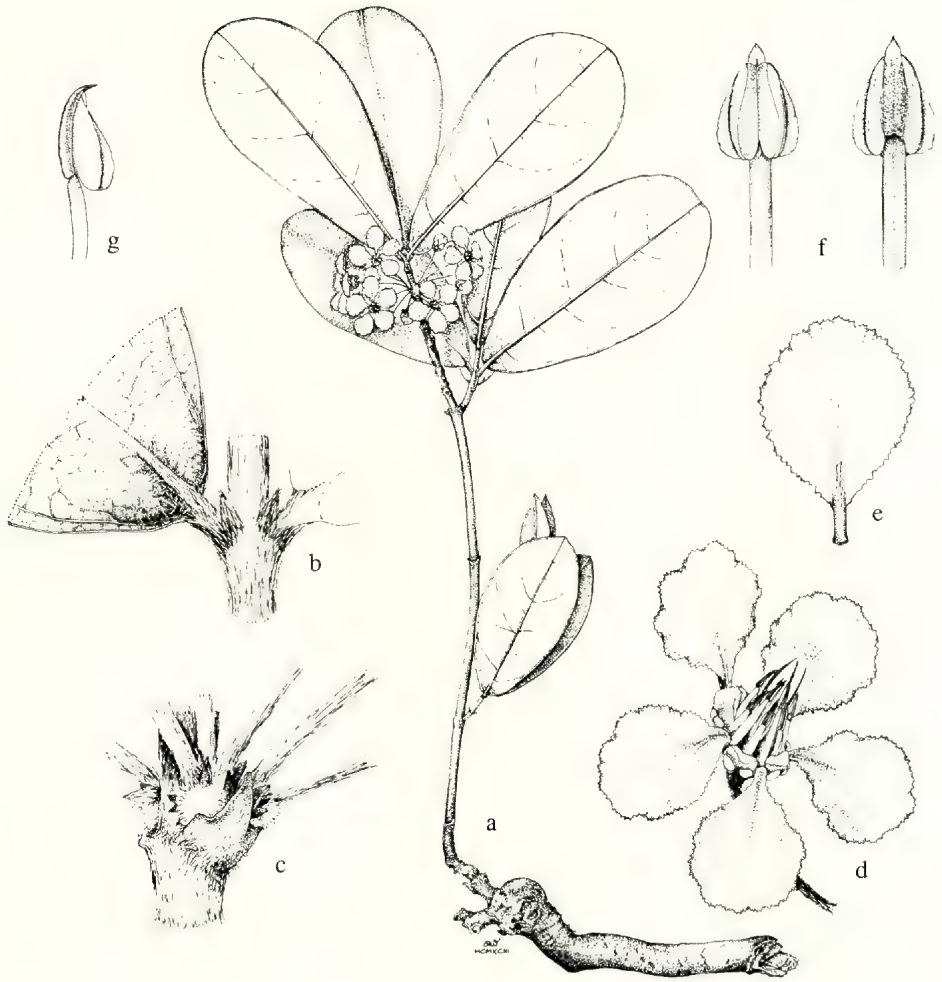

FIG. 8. *Pterandra hatschbachii*. a) habit, ×0.5; b) leaf bases showing stipules and inflated areas at base of lamina, ×5; c) base of fascicle of flowers showing bracts and bracteoles and large bract subtending whole fascicle, this usually deciduous by anthesis, ×5; d) flower with posterior petal at upper left, ×2.5; e) posterior petal, abaxial view showing sparse hairs on midrib, ×3.5; f) anthers, flattened, adaxial view (left) and abaxial view (right), ×7.5; g) anther, side view, ×7.5. Drawn by Karin Douthit, a–b and d–g from *Hatschbach 35085*, c from *Hatschbach 33276*.

I am happy to name this plant for my friend Gert Hatschbach of the Museu Botânico Municipal in Curitiba, whose eagle-eye has led him to so many first collections of undescribed species. *Pterandra hatschbachii* is to be compared to *P. pyroidea* Adr. Juss., a plant of the cerrados of central Brazil. They are similar in producing aerial shoots from a low woody stem that may be subterranean, and *P. pyroidea* usually has obovate leaves with very short petioles. Its petals are pink, and its anthers are deciduous and have a short triangular apical extension of the connective. But *P. pyroidea* is a much more robust plant than *P. hatschbachii*, its erect stems typically 0.5–1 m tall and 2.5–6 mm in diameter. Stem and leaf hairs are much more serpentine or twisted, producing a less appressed vesture, the leaves are usually much hairier, at least initially, and the strongly scalariform tertiary veins are usually prominent below, much more than the rest of the reticulum. Also, the petals of *P. pyroidea* are usually hairier abaxially than those of *P. hatschbachii*.

Tetrapterys monteverdensis W. R. Anderson, sp. nov.—TYPE: COSTA RICA. Puntarenas: Monteverde Cloud Forest Reserve, Sendero Pantanoso, swampy area on continental divide, lower montane rain forest, 10°20' N, 84°50' W, 1500–1600 m, Jun fl, *Haber ex Bello 5217* (holotype: MICH!).

Liana lignosa, ramis appresso-tomentosis, demum verruculosis. Lamina foliorum majorum 8–16 cm longa, 4.5–7.2 cm lata; stipulae in paribus interpetiolaribus connatae, pari 4–6 (–7.5) mm longo, 1.2–3 mm lato, anguste triangulari. Sepala abaxialiter glabra vel sparsim sericea in dimidio distali. Petala lateralia ungue 1.5–2.5 mm longo, limbo 6–10 mm longo, 4–8 mm lato; petalum posticum ungue 2–2.8 mm longo, limbo 5–5.5 mm longo, 4–5 mm lato. Samara alis lateralibus liberis, 2 superioribus 25–48 mm longis, 10–17 mm latis, 2 inferioribus 10–30 mm longis, 6–13 mm latis.

Woody vine; stems densely appressed-tomentose with several layers of hairs with sinuous to nearly straight crosspieces, those of the outer layer with a definite slender stalk; older stems roughened by tiny bumps or pegs (persistent hair bases) after hairs fall. Lamina of larger leaves 8–16 cm long, 4.5–7.2 cm wide, ovate or elliptical, rounded or subcordate at base, obtuse, acute, or acuminate at apex, initially sericeous above but very soon quite glabrate, loosely sericeous to glabrate below with the hairs stramineous or white, those of the lamina surface 0.4–1.2 mm long, those persistent on midrib straight but at least some short-stalked and somewhat spreading, the abaxial glands 1–several near base and none or few on proximal 1/3 of lamina, the reticulum of fine veinlets prominent on both sides; petiole 8–15 mm long, eglandular, loosely sericeous to glabrate; stipules connate in interpetiolar pairs, the pair 4–6 (–7.5) mm long, 1.2–3 mm wide, smaller in inflorescence, narrowly triangular, abaxially sericeous. Inflorescence appressed-tomentose like stem, cymose-paniculate with the branches terminating in an umbel of 4 flowers; floriferous bracts 1.5–2.5 mm long, ovate, sparsely sericeous to glabrate; peduncle 3–5.5 mm long, persistently tomentose; bracteoles 1–1.5 mm long, ovate, apical; pedicel 3–7 mm long, tomentose or velutinous to glabrescent even before anthesis. Sepals ca 1 mm long beyond glands, ca 1.5–2 mm wide, broadly rounded, abaxially glabrous or only sparsely sericeous beyond glands, adaxially glabrous, pressed against filaments in anthesis, the anterior eglandular, the lateral 4 biglandular with the glands 2.7–4 mm long, obovate. Petals yellow, turning orange in age, glabrous, erose, nearly truncate at base, the lateral 4 reflexed, with claw 1.5–2.5 mm long and limb 6–10 mm long, 4–8 mm wide; posterior petal erect, with claw 2–2.8 mm long and limb 5–5.5 mm long, 4–5 mm wide. Filaments 2–3 mm long, glabrous except for tufts of hair abaxially at base, nearly straight, 1/3–1/2 connate; anthers 1.3–2 mm long, glabrous, more or less alike, the connective swollen. Ovary 1.5–2 mm high, sericeous, prominently crested; styles 2.3–3 mm long, sericeous at base, the anterior style slightly shorter and slenderer than the posterior 2. Samara tomentose or subsericeous, the lateral wings distinct, the upper ones 25–48 mm long and 10–17 mm wide, the lower ones 10–30 mm long and 6–13 mm wide; dorsal wing 3–6 mm wide, entire or slightly erose; nut smooth between dorsal and lateral wings.

ADDITIONAL SPECIMENS EXAMINED. **Costa Rica**. GUANACASTE: Río Negro, Tilarán, Finca Hermanos Bello, 10°21' N, 84°49' W, 1400 m, May fl, *Haber 7141* (MO).—PUNTARENAS, Monteverde: lower montane rain forest, 1550 m, Aug fr, *Gentry et al. 48834* (MICH); lower montane wet forest, 1550 m, Sep fr, *Haber 2811* (MICH); Pacific slope, lower montane wet forest, 1400 m, Jun fl, *Haber ex Bello 5061* (MO); upper San Luis river valley on Pacific slope, moist to wet forest transition, 1300–1400 m, Aug fr, *Haber ex Bello et al. 5408* (CR, MICH).

This is a species of section *Lophogynixa* Nied., apparently endemic to the region of Monteverde, for which it is named. *Tetrapterys monteverdensis* is distinguished by its stalked stem hairs that leave the stem verruculose, the relatively small leaves, the long narrow stipule-pairs, the distally glabrous sepals, the large petals, and the large samaras. Its high-elevation habitat also merits mention.

Tetrapterys skutchii W. R. Anderson, sp. nov.—TYPE: COSTA RICA. San José: vicinity of El General, 975 m, Aug fl, *Skutch 2808* (holotype: NY!).

Rami dense sericei. Lamina foliorum majorum 10.5–13.2 cm longa, 5.2–6.9 cm lata, obovata, basi cuneata, apice acuminata, subtus sericea vel glabrata pilis flavis, rectis, sessilibus, appressis, 1–1.5 mm longis; stipulae in paribus interpetiolaribus connatae, pari 2–3 mm longo, 1.5 mm lato, triangulari. Inflorescentia laxe aureosericea, floribus in umbellis 4-floris, pedunculo 3–9 mm longo, pertinaciter sericeo, pedicello 4–5 mm longo, tomentoso mox glabrescenti. Sepala abaxialiter dense aureosericea. Antherae pilosae, inter loculos sericeae. Stylus anticus valde redactus, per anthesin non visibilis.

Woody vine (?); stems densely sericeous, the hairs straight, sessile, appressed, leaving tiny pegs after falling. Lamina of larger leaves 10.5–13.2 cm long, 5.2–6.9 cm wide, obovate, cuneate at base, acuminate at apex, initially sericeous but soon glabrate above, sericeous to glabrate below with the hairs golden, straight, sessile, appressed, 1–1.5 mm long, without large glands at base but with a row of small impressed glands below parallel to but set well in from the margin, extending the whole length of the lamina, the reticulum prominent on both sides; petiole 7–9 mm long, eglandular, persistently sericeous; stipules connate in interpetiolar pairs, the pair 2–3 mm long, 1.5 mm wide, triangular, abaxially sericeous. Inflorescence (including all the axes distal to the last pair of full-sized leaves) golden-sericeous with several layers of hairs adding appreciably to diameter of axis, the outermost layer relatively loosely appressed, cymose-paniculate with the branches terminating in an umbel of 4 flowers; floriferous bracts 1.3–2 mm long, ovate, abaxially sericeous, adaxially glabrous; peduncle 3–9 mm long, persistently loosely sericeous or subtomentose; bracteoles 1–1.5 mm long, ovate, apical; pedicel 4–5 mm long, appressed-tomentose to glabrescent already in anthesis. Sepals ca 1 mm long beyond glands, ca 2 mm wide, broadly obtuse or rounded, very thick, incurved in anthesis, abaxially so densely golden-sericeous as to completely conceal all sepal tissue, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with glands ca 3.5 mm long, elliptical. Petals yellow, glabrous, erose, sagittate at base, the lateral 4 reflexed, with claw 1.5 mm long and limb 5.5–6.5 mm long, 4–6 mm wide; posterior petal erect, with claw 2 mm long and limb 4.5 mm long, 4 mm wide. Filaments 1.7–2 mm long, glabrous except for tufts of hair abaxially at base, straight, ca 1/2 connate; anthers 1.4–1.6 mm long, loosely pilose, especially at base and apex, and densely sericeous between locules, the connective dark red. Ovary ca 1.3 mm high, sericeous; styles straight, the posterior 2 ca 2 mm long, stout and visible above anthers, the anterior style only 1 mm long, very slender, pressed between the other 2 and hidden by stamens, not evident in open flower. Fruit not seen.

This species is named for Alexander F. Skutch, collector of the type and only known specimen. *Tetrapterys skutchii* belongs to section *Lophogynixa*, within which it is allied with *T. donnell-smithii* Small. It is distinguished from that and similar species by its abundantly pilose anthers, a most unusual feature in the genus. It is

also notable for the long, straight, sessile, appressed leaf hairs, the golden, moderately loose vesture of the inflorescence, the abaxially densely sericeous sepals, and the much-reduced anterior style.

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THE IDENTITIES OF THE SERICEOUS-LEAVED SPECIES OF STIGMAPHYLLON (MALPIGHIACEAE) IN THE AMAZON REGION

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INTRODUCTION

Stigmaphyllon, one of the Neotropical wing-fruited genera of the Malpighiaceae, includes nearly 100 species. Most are characterized by long-petioled broad leaves, yellow flowers grouped in umbels or pseudoracemes disposed in dichasially branched inflorescences, an androecium of 10 heteromorphic stamens, and a gynoecium whose 3 styles bear apical appendages, the folioles, for which the genus is named. The samara usually consists of an ovoid nut with a large flaring dorsal wing and often also with lateral ornamentation (one to several small lateral winglets, spurs, and/or crests). Both nomenclatural and taxonomic problems have confused the identities of some of the representatives occurring in the Amazon region in which the leaves are sericeous below, i.e., the trabecula of the hair straight and sessile to subsessile. This group of plants was found to comprise four species, *S. argenteum* C. Anderson (recently described), *S. cardiophyllum* Adr. Juss. (a name long ignored), *S. convolvulifolium* Adr. Juss. (the epithet traditionally attributed to Cavanilles), and *S. sinuatum* (DC.) Adr. Juss. (a name long misapplied). For these, the names *S. brachiatum* Tr. & Pl., *S. convolvulifolium* Adr. Juss., *S. fulgens* Adr. Juss., *S. hypoleucum* Miquel, *S. martianum* Adr. Juss., and *S. splendens* Cuatr. have been most commonly used. These four species are discussed here in detail. Four sympatric species, *S. lacunosum* Adr. Juss., *S. maynense* Huber, *S. paraense* C. Anderson, and *S. puberum* (Rich.) Adr. Juss. are included in the key presented below; although distinctive, they are occasionally confused with one of the other four, because they also have abaxially sericeous leaves.

The very different *S. paralias* Adr. Juss., also with the leaves sericeous below, is unlikely to be confused with any other species of the genus. It is mentioned here, because it has been recorded from the area of Tucuruí in Pará, Brazil. *Stigmaphyllon paralias* is a shrub of dry and sandy areas of eastern Brazil from Maranhão to Rio de Janeiro. Its usually elliptical to lanceolate leaves have very short petioles (up to 1.5 cm long), and the stipules are often fused across the node into a bifid structure. The inflorescence is most commonly a solitary umbel of (3–) 4–15 large flowers or sometimes a dichasium of umbels. The peduncles are very short, only 0.02–0.2 times as long as the pedicels. The greatly modified "samara" consists of a nut lacking a carpophore and bearing an apical crest, the rudimentary dorsal wing.

TAXONOMY

[Note: Atypical specimens of *S. cardiophyllum* from Ecuador, considered putative hybrids, may not key here; see discussion below under *S. cardiophyllum*.]

1. Anthers pubescent.
   2. Laminas very sparsely sericeous to glabrous below, margin with irregularly spaced sessile glands and the bases of broken-off filiform glands; anthers of stamens opposite the posterior-lateral sepals with the connective enlarged and bearing only one locule; dorsal wing of the samara 2.7–4 cm long, the nut 2.5–3.5 mm in diameter, without air chambers; along river banks in lowland and flood plain forest, at forest edge, and in secondary growth and capoeiras of Amazonian Ecuador, Peru, Brazil, and Bolivia. *S. cardiophyllum* Adr. Juss.
   2. Laminas evenly sericeous below; marginal glands nail-like, i.e., a disk borne on a stalk up to 0.5 mm long (sometimes a few glands sessile); anthers of stamens opposite the posterior-lateral sepals not modified, the connective and both locules subequally long; dorsal wing of the samara reduced and ca. 2 cm high measured from base of nut, the nut ca. 12.5 mm in diameter, the locule surrounded by air chambers; along river banks and in inundated forest in Amazonian Brazil and Peru. *S. lacunosum* Adr. Juss.
1. Anthers glabrous.
   3. Anterior style and its opposing stamen much larger than the posterior styles and their opposing stamens; posterior styles foliolate.
      4. Laminas sparsely sericeous below or rarely the hairs more abundant but the epidermis always visible; petals digitate-fimbriate; dorsal wing of samara erect and tapered from the base, lateral winglets and carpophore absent; in rain forests and gallery forests, along river banks, and in mangrove swamps in the West Indies, Central America, and northern South America (not reported from Ecuador): Venezuela (Delta Amacuro, Monagas), Guyana, French Guiana, Colombia (northernmost Chocó and Antioquia, Putumayo), Peru (northern Loreto, Huánuco), Amazonian Brazil (Amapá, Pará, Amazônas, Acre). *S. puberum* (Rich.) Adr. Juss.
      4. Laminas very densely sericeous below, the epidermis obscured; petals erose to erose-denticulate; dorsal wing of samara flared distally, the nut bearing 3–4 lateral winglets per side, carpophore present; in wet forests and at water's edge in Ecuador (Napo, Pastaza) and Peru (Amazonas, Huánuco, Loreto, San Martín, Pasco, Madre de Dios), one collection from Brazil (southwestern Amazônas). *S. maynense* Huber.
   3. Anterior style and its opposing stamen shorter than or at most subequal to the posterior styles and their opposing stamens; posterior styles foliolate or efoliolate.
      5. Stamens opposite the posterior-lateral sepals subequal to the stamen opposite the posterior petal (flag), their anthers unmodified.
         6. Laminas appearing glabrous below to the naked eye, but often very sparsely sericeous, the hairs ca. 0.1 (–0.2) mm long and widely spaced, never touching; in moist forest, along rivers, and also in secondary growth and along roadsides in Guyana, Suriname, French Guiana, and northeastern Brazil (Amapá and eastern Pará), also recorded from Martinique and Trinidad. *S. convolvulifolium* Adr. Juss.
         6. Laminas sparsely to very densely sericeous below, the hairs (0.2–) 0.3–0.5 (–0.7) mm long, usually touching to overlapping; common in primary and secondary forest, especially wet forest, along rivers, in thickets, and at roadsides in Colombia, Venezuela, the Guianas, northern Brazil, Ecuador, northern Peru, and Amazonian Bolivia. *S. sinuatum* (DC.) Adr. Juss.
      5. Stamens opposite the posterior-lateral sepals unlike the stamen opposite the posterior petal (flag), their anthers modified: the connective enlarged and bearing 0–2 reduced locules.
         7. Limb of lateral petals 6–7 mm in diameter, erose; nut of samara without lateral winglets and air chambers; in forests and thickets and at roadsides of eastern Peru (Huánuco, Junín, Loreto, Pasco, San Martín). *S. argenteum* C. Anderson.
         7. Limb of lateral petals 10–15 mm in diameter, with fimbriae up to 0.8 mm long; nut of samara with one or more pairs of lateral winglets, locule surrounded by air chambers; in woods along rivers, in wet localities in savanna and campo, and in várzea of Brazil (Goiás, Maranhão, western Piauí, Pará). *S. paraense* C. Anderson.

Stigmaphyllon argenteum C. Anderson, Novon 2: 302. 1992.—TYPE: PERU. Huánuco: Prov. Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abejas, 1 km arriba del pueblo Tournavista o unos 20 km arriba de la confluencia con el Río Ucayali, 300–400 m, 30 May 1967, *Schunke V. 2018* (holotype: NY!; isotypes: COL! F! G! US!). Fig. 1.

Vine to 14 m. Laminas 2.5–15.3 cm long, 5.7–14 cm wide, triangular, ovate, elliptical to suborbicular, or sometimes 3–5-lobed, apex acuminate, base truncate to cordate, sparsely sericeous to usually glabrous above, sericeous below (trabecula 0.2–0.5 mm long, straight, sessile), margin with irregularly spaced sessile glands (0.5–0.6 mm in diameter) and with filiform glands (up to 1.5 mm long), with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.5–3.5 mm in diameter; petioles 2–10+ cm long; stipules 0.7–1.2 mm long and wide, eglandular. Flowers ca. 15–30 per umbel, these borne in dichasia or compound dichasia. Peduncles 3–7.5 mm long, pedicels 4–8.5 mm long; peduncles 0.6–1.2 times as long as the pedicels. Bracts 0.9–1.3 mm long, 0.6–1 mm wide, narrowly triangular; bracteoles 0.7–1.2 mm long, 0.6–1 mm wide, triangular, eglandular. Sepals 1.8–2.3 mm long, 1.5–2 mm wide, glands 1.6–2.3 mm long, 0.6–1.2 mm wide. Lateral petals with the limbs orbicular or broadly obovate, glabrous, yellow, margin erose; anterior-lateral petals: claw 1.8–2.2 mm long, limb ca. 7 mm long and wide; posterior-lateral petals: claw 0.5–1 mm long, limb 6–6.7 mm long, 4.5–6 mm wide; posterior petal: claw 2.5–2.8 mm long, apex strongly indented, limb 5–5.6 mm long, 3.5–4.8 mm wide, elliptical or broadly obovate, margin erose to fimbriate-denticulate, teeth/fimbriae up to 0.5 mm long. Stamens unequal, those opposite the posterior styles the largest, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers all loculate, glabrous, those of stamens opposite the anterior-lateral sepals with 1 or 2 locules, those of stamens opposite the posterior-lateral sepals with only 1 locule. Anterior style ca. 2.2 mm long, shorter than the posterior two, glabrous; apex ca. 1.5 mm long, each foliole ca. 1.4 mm long, ca. 1.2 mm wide, subsquare. Posterior styles 2.6–3 mm long, glabrous, lyrate; foliole ca. 1.4–2 mm long and wide, subsquare. Dorsal wing of samara ca. 4.5 cm long, 1.4–1.7 cm wide, upper margin with a blunt tooth, lateral winglets absent, nut only prominently ribbed; nut 4–5.5 mm high, 3.5–4.5 mm in diameter, areole 3–3.5 mm long, 2.5–2.8 mm wide, concave, carpophore up to 1.8 mm long. Embryo 5.8–7.3 mm long, ca. 2 times as long as wide, ovoid, outer cotyledon 6.1–8.3 mm long, 2.6–3.9 mm wide, the distal 1/6 folded over the inner cotyledon, inner cotyledon 4–6.6 mm long, 2–3.6 mm wide, straight or the tip folded back on itself.

Phenology. Collected in flower from April through July; in fruit in May and from July through September.

Distribution. Lowlands of eastern Peru; in forests and thickets and at roadsides; 135–670 m.

REPRESENTATIVE SPECIMENS. **Peru.** HUÁNUCO: Prov. Pachitea, region of Pucallpa, ca. 26 km S to 24 km SSE of Puerto Inca, N of Río Yuyapichis, 09°37'–09°34'S, 74°56'–74°53'W, *Wallnöfer 11-31588* (MICH); vicinity of Tingo María, 3–5 km from Huánuco-Tingo María rd on Monzón rd, *Mathias & Taylor 3647* (F, UCLA).—JUNÍN: Puerto Bermudez, *Killip & Smith 26630* (F, NY, US); Prov. Satipo, E bank of Río Ene at mouth of Río Quipachiari, *Madison 10427-70* (F).—LORETO: Quebrada Shanuce above Yurimaguas, *Croat 17999* (MICH); Isla de Ushpa-cano near mouth of the

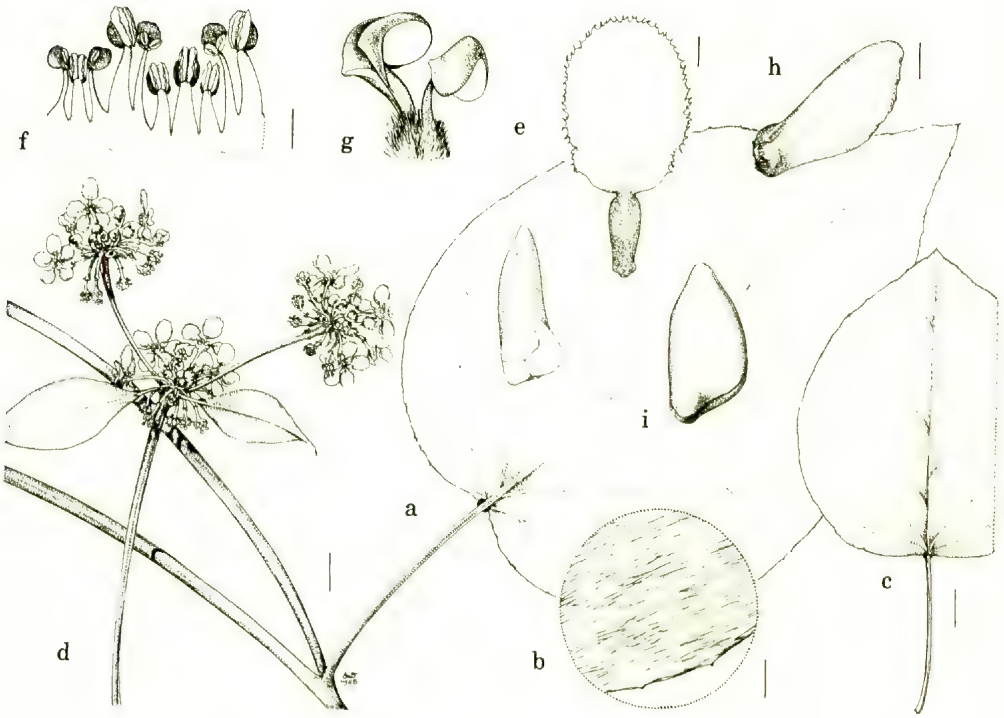

FIG. 1. *Stigmaphyllon argenteum*. a. Portion of branch with large leaf. b. Detail of abaxial surface of lamina. c. Small leaf. d. Flowering branch. e. Posterior petal. f. Androecium, second stamen from left opposes posterior petal. g. Gynoecium, anterior style to the right. h. Samara. i. Two views of an embryo. Scale for a, c, d, h, bar = 1 cm; for b, bar = 0.5 mm; for e–g, bar = 1 mm. (Based on: a, b, d–g, *Schunke V. 2018*; c, h, i, *Croat 19640*.)

Río Itaya, *Croat 19640* (MICH); Ucayali, Bosque Nacional Alexander von Humboldt, between Km 90–130 of Pucallpa-Tingo María rd, 08°48'S, 75°20'W, *Gentry et al. 41413* (MO); wooded banks on lower Río Huallaga, *Killip & Smith 29004* (F, GH, NY); Prov. Maynas, vicinity of Iquitos, Río Momón, quebrada Momoncillo, *McKenna et al. DMK-91* (AMAZ, F, MICH, MO).—Pasco: Oxapampa, ca. 5 km up Río Iscozacín from village of Iscozacín, 10°12'S, 75°13'W, *Knapp & Staver 7802A* (MICH); Palcazu Valley, Río San José in the Río Chuchurras drainage, 10°09'S, 75°20'W, *D. Smith 4002* (MICH).—San Martín: between Tocache Nuevo and Juanjui, 18.7 km S of Río Pulcache, 07°55'S, 76°40'W, *Croat 58052* (MICH); vicinity of Aguaytía, Boquerón de Padre Abad, *Mathias & Taylor 3591, 6092* (F, UCLA); Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, quebrada de Santiago, al E de Puerto Pizana, *Schunke V. 6530* (GH, MO); Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, quebrada de Cachiyaca, afluente de la quebrada de Huaquista, al E de Puerto Pizana, *Schunke V. 8528* (F, MICH, MO).

Stigmaphyllon argenteum is named for the silvery pubescence on the abaxial leaf surfaces. It is distinguished by its small flowers, in which the petal limbs are only up to 7 mm in diameter and the anthers of stamens opposite the posterior-lateral sepals bear only one locule, and by its samaras, which lack lateral winglets. *Stigmaphyllon cardiophyllum* differs in its abundantly pubescent anthers and its leaves, which may be very sparsely sericeous below but most commonly are glabrate to glabrous. In *S. sinuatum*, the flowers are borne in pseudoracemes instead of umbels, the petals are usually larger (up to 13 mm in diameter), the stamens opposite the posterior-lateral sepals have unmodified anthers and are subequal to the stamen opposite the posterior petal, the styles are commonly pubescent (glabrous in *S. argenteum)*, and the nut of the samara usually bears lateral winglets. *Stigmaphyllon convolvulifolium* and *S. argenteum* are not sympatric.

Stigmaphyllon cardiophyllum Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840.—TYPE: "Brasilia borealis," collector unknown (holotype: P!, photos: F! MICH!, fragment: P-JU!). Fig. 2.

Vine to 15 m. Laminas 7.3–17 cm long, 3.7–13.5 cm wide, ovate to elliptical (the smaller often narrowly elliptical) to suborbicular, sometimes shallowly to deeply 2–3-lobed, apex acuminate to acuminate-caudate, base truncate to cordate or sometimes attenuate, especially in smaller laminas, very sparsely sericeous to glabrous above and below (trabecula 0.2–0.9 mm long, straight, sessile to subsessile), margin with irregularly spaced sessile glands (0.2–0.6 mm in diameter) and the bases of broken-off filiform glands, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.1–3 mm in diameter; petioles 2.7–8 cm long; stipules 0.5–1 mm long, 0.5–1.4 mm wide, eglandular. Flowers ca. 15–25 (–30) per umbel, these borne in dichasia or compound dichasia or small thyrses. Peduncles (1.5–) 2.2–5 mm long, pedicels 4–10 mm long; peduncles 0.3–1 times as long as the pedicels. Bracts 0.7–2 mm long, 0.5–0.8 mm wide, triangular or narrowly so; bracteoles 0.4–1 mm long, 0.4–0.8 mm wide, triangular, usually eglandular or sometimes each bracteole with a pair of inconspicuous glands (each ca. 0.1 mm in diameter). Sepals 1.2–2 mm long and wide, glands 1–1.8 mm long, 0.7–1 mm wide. All petals with the limbs glabrous, yellow; lateral petals with the limbs orbicular, margin erose; anterior-lateral petals: claw 1–1.8 (–2.1) mm long, limb (5–) 6–6.5 mm long and wide; posterior-lateral petals: claw 0.5–1 (–1.3) mm long, limb 4–5 mm long and wide; posterior petal: claw 2–2.5 mm long, apex indented, limb (3.2–) 3.5–4 mm long, (2.3–) 3–4 mm wide, broadly obovate to broadly elliptical to suborbicular, margin irregularly denticulate to denticulate-erose to sometimes erose. Stamens unequal, those opposite the posterior styles the largest but their filaments subequal to those of stamens opposite the anterior-lateral sepals, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced, those opposite the posterior-lateral sepals usually with only 1 tiny locule; anthers all loculate, pubescent. Anterior style 2–2.3 mm long, shorter than the posterior two, glabrous; apex 0.9–1.1 mm long; each foliole 0.5–0.8 mm long, 0.4–0.8 mm wide, triangular to square. Posterior styles 2.2–2.6 mm long, glabrous, lyrate; foliole 0.9–1.2 mm long, 0.8–1.4 mm wide, subsquare to subtrapezoidal. Dorsal wing of samara 2.7–4 cm long, 1.1–1.8 cm wide, upper margin with a blunt tooth; lateral winglets absent, nut only prominently ribbed; nut 4.1–5.5 mm high, 2.5–3.5 mm in diameter, areole 2.5–3.3 mm long, 2.1–2.5 mm wide, convex, carpophore up to 3 mm long. Embryo 4.5–6.4 mm long, ca. 2 times as long as wide, ovoid, outer cotyledon 4.2–5.9 mm long, 2.5–3.1 mm wide, straight, inner cotyledon 3.9–5.5 mm long, 1.8–2.8 mm wide, straight.

Phenology. Collected in flower from May through February, in fruit from June through April.

Distribution. Amazonian lowlands of Ecuador, Peru, Brazil, and Bolivia; along river banks in lowland and floodplain forest, at forest edge, and in secondary growth and capoeiras; sea level to 1600 m.

REPRESENTATIVE SPECIMENS. **Ecuador.** NAPO: Estación Biológica Jatun Sacha, 8 km al este de Misahuallí, 01°04'S, 77°36'W, *Cerón M. & Iguago 5592* (MICH); Río Napo, Puerto Napo, *Harling 3518* (S); Misahuallí, *Steiner 275* (MICH).—PASTAZA: Puerto Sarayacu, *Lugo S. 3899* (GB, MICH). **Peru.** AMAZONAS: Río Cenepa, vicinity of Humapimi, ca. 5 km E of Chávez Valdivia, ca. 04°30'S, 78°30'W, *Ancuash 1134* (F, MICH, MO); Valle de Santiago, Quebrada Caterpiza, 03°50'S, 77°40'W, *Tunqui 708* (MICH, MO); Aramango, *Woytkowski 5629* (G, GH, MO, US).—CUZCO: Prov. Paucartambo, Atalaya, near junction of Río Carbón and Río Alto Madre de Dios, *Foster 3041* (MICH).—

FIG. 2. *Stigmaphyllon cardiophyllum*. a. Flowering branch (×0.5). b. Detail of abaxial leaf surface (×5). c–f. Leaves illustrating variation of laminar shape (×0.5). g. Posterior petal (×2.5). h. Androecium (×10), second stamen from left opposes posterior petal. i. Gynoecium (×7.5), anterior style at center. j. Samara (×1). k. Embryo (×2.5). (Based on: a, b, f–i, *Encarnación 26052*; c, *Ancuash 1134*; d, *Woytkowski 5954*; e, *Nee 36821*; j, k, *Foster 6506*.)

HUÁNUCO: Tingo María, *Asplund 12103* (S); Prov. Huánuco, Maranjillo, cerca a Tingo María, *Ferreyra 2196* (MICH); 69 km NE of Tingo María on rd to Tocache, Huallaga Valley, ca. 09°S, 76°W, *Gentry et al. 37633* (MICH).—JUNÍN: Sani Beni, *Woytkowski 5954* (GH, MO, US); Mazamari, *Woytkowski 5979* (MO, US); San Ramón, *Woytkowski 7412* (GH, MO).—LORETO: Alto Amazonas, Dtto. Pastaza, Río Pastaza, *Ayala 2295* (AMAZ, MICH); Coronel Portillo, Tournavista, márgen izquierda del Río Pachitea, *Encarnación 26052* (MO, NY); Prov. Coronel Portillo, Bosque Nacional de von Humboldt, Km 86, Pucallpa-Tingo María rd, 08°40'S, 75°00'W, *Gentry & Horner 29481* (AMAZ, MICH); Mishuyacu, near Iquitos, *Klug 160* (F, NY, US); Stromgebiet des Marañón von Iquitos aufwärts bis zur Santiago-Mündung am Pongo de Manseriche, 77°30'W, *Tessman 3966* (G, S); Prov. Maynas, Iquitos, Quistacocha, 03°48'S, 73°25'W, *Vásquez & Jaramillo 12072* (MICH).—MADRE DE DIOS: Prov. Tambopata, Lago Tres Chimbadas, ca. 65 river km SSW of Puerto Maldonado, ca. 10–15 air km NW effluence Río La Torre (Río D'Orbigny)/Río Tambopata, 12°49'S, 69°17'W, *Barbour 5744* (MICH); Prov. Manu, Parque Nacional del Manu, Río Manu, Cocha Cashu Station, 11°50'S, 71°25'W, *Foster 6506* (F), *9704* (F, MICH); small tributary of Río Madre de Dios, 1 km below Puerto Maldonado, *Gentry et al. 19654* (F, MICH).—SAN MARTÍN: Prov. Mariscal Cáceres, entre Pólvora y Chiote, valle Huallaga, *Ferreyra 4464* (MICH, US); Prov. San Martín, cerca de Shapaja, *Ferreyra 18273* (US); Tarapoto, *Ule 6438* (G, K, MG, NY); Pona to Saposoa, *Woytkowski 5442* (F, MO). **Brazil.** ACRE: 9 km from Rio Branco on Rio Branco-Porto Acre rd, *Lowrie 646* (INPA, MICH); Mpio. Serra Madureira, Rio Caeté, afluente do Rio Iaco, *Raos et al. 643* (INPA); Rio Juruá-Juruá Mirim, *Ule 5593* (G, MG).—AMAZONAS: Bôca do Acre, Purús, *Goeldi 3969* (MG); Tonantins (Solimões), *Jobert 764* (P); Mpio. São Paulo de Olivença, near Palmares, *Krukoff 8291* (A, BR, F, G, LE, MICH, MO, NY, P, S, U).—MARANHÃO: between Viana and Banderante, ca. 03°00'S, 45°10'W, *Daly et al. 648* (NY); Alzilândia, Rio Pindaré, 03°45'S, 46°05'W, *Jangoux & Bahia 321* (MICH).—PARÁ: Alenquer, Colônia Lauro Sodré, Km 15, *Fróes 29378* (IAN); Ilha de Mosqueiro, near Pará, *Killip & Smith 30394* (NY); Rd BR-22, Capanema to Maranhão, Km 96, *Prance & Pennington 1824* (IAN, MICH, NY). **Bolivia.** BENI: Bopi River valley, *Rusby 385* (K, MICH, NY, US).—LA PAZ: Prov. Sud Yungas, Alto Beni, carretera entre Puente Sapecho y Santa Ana, *Seidel & Schulte 2301* (MICH); Prov. Nor Yungas, Alto Beni, camino del puente hacia San Antonio, *Seidel & Schulte 2320* (MICH).—PANDO: Prov. Manuripi, antes de Independencia, *Moraes 264* (MICH); Prov. Manuripi, along Río Madre de Dios, 80 km (by air) downstream from and W of Chibe, 11°54'S, 68°02'W, *Nee 31525* (MICH); Río Acre, im Walde bei Cobija, *Ule 9484* (G, K, MG).—SANTA CRUZ: Prov. Andrés Ibánez, 12 km E of center of Santa Cruz on rd to Cotoca, 17°46'S, 63°04'W, *Nee 36821* (MICH).

Stigmaphyllon cardiophyllum, a common species of the Amazonian lowlands, is readily recognized by its very sparsely sericeous to usually glabrous leaves, small flowers, and samaras. The laminas are mostly ovate to elliptical (the smaller narrowly so) and only sometimes cordate, as in the type. The limbs of the petals are only up to 6.5 mm in diameter. The anthers are pubescent, and those opposite the posterior-lateral sepals bear only one tiny locule (very rarely two). The samara lacks lateral ornamentation. This species may be confused with forms of *S. sinuatum* with abaxially very sparsely pubescent leaves, and, in eastern Brazil (Pará), with *S. convolvulifolium*, whose leaves are also very sparsely sericeous to glabrous below. Both differ in their larger flowers (limbs of the petals up to 15 mm in diameter), glabrous anthers (all with two locules), usually pubescent styles (glabrous in *S. cardiophyllum*), and samaras that are usually laterally ornamented with winglets, crests, and/or spurs. For a separation from S. *argenteum*, see that species.

Several collections from Ecuador and one from Peru may represent hybrids between *S. cardiophyllum* and an unknown species, possibly the sympatric *S. sinuatum*. They differ from typical specimens of *S. cardiophyllum* in their leaves, anthers, posterior styles, and, sometimes, the samaras. The laminas are persistently sparsely sericeous below (the trabecula 0.3–0.5 mm long, sessile). The anthers are only sparsely pubescent or glabrous, and those of the posterior-lateral stamens may have two unequal locules. The posterior styles are sparsely pubescent in the proximal 1/3, and the nut of the samara may have a small lateral winglet or

spur. Pollen of these anomalous specimens is mostly composed of misshapen, heavy-walled grains. When placed in cotton blue in lactophenol, only 0–20% of the pollen is stained; the grains that do stain are of unequal size. The following collections are considered putative hybrids:

Ecuador. MORONA-SANTIAGO: alrededores del puente sobre el Río Bombioza, carretera Gualaquiza-Zamora cerca la Paroquia de Bombioza, *M. Baker 6479* (MICH).—NAPO: Estación Biológica Jatun Sacha, 8 km al este de Misahuallí, 01°04'S, 77°36'W, *Cerón M. 2038* (MICH); Payamino, Reserva Floristica "El Chuncho," 5 km al NW de Coca, 00°30'S, 77°01'W, *Cerón M. & Neill 2367* (MICH); vía Puerto Napo-Misahuallí, *Jaramillo 87* (AAU, NY, QCA); Río Napo between Coca (Puerto Francisco de Orellana) and Armenia Vieja, *Harling & Andersson 11977* (GB, MICH); Santa Rosa at Río Napo, *Lugo 168, 1981, 2001, 2027* (GB, MICH); Misahuallí at Río Napo, *Lugo 2273* (GB, MICH).—ZAMORA-CHINCHIPE: near Méndez, *Camp E-853* (NY, US). **Peru.** AMAZONAS: Río Cenepa, vicinity of Huampami, ca. 5 km E of Chávez Valdívia, ca. 04°30'S, 78°30'W, *Ancuash 1262* (F, MICH, MO).

The name *Stigmaphyllon cardiophyllum* has long been ignored, because most later botanists did not see Jussieu's type and found his description not definitive enough to assign this name with confidence. Collections of this species were often left undetermined, assigned to *S. convolvulifolium*, or labeled with one of the synonyms of *S. sinuatum*. Grisebach (1858) did recognize *S. cardiophyllum* and correctly listed a Spruce collection with heart-shaped leaves from Bentham's herbarium (*Spruce 1644*, K!); however, Niedenzu (1900) tentatively placed *S. cardiophyllum* in *S. salzmannii* Adr. Juss. Niedenzu later (1928) listed *S. cardiophyllum* as a separate species but only quoted Jussieu's description from the *Monographie* (1843) and cited Grisebach (1858). Macbride (1949) included *S. cardiophyllum* at the species level in his account of the Malpighiaceae of Peru. He noted that *Williams 6883* was distributed as *S. cardiophyllum* [correctly identified, F!], but that it "is probably referable to *S. tiliaefolium* or allied form." He cited other collections of *S. cardiophyllum* under other names, e.g., *Tessmann 3412* (NY!) and *3966* (G! S!) as *S. convolvulifolium*, and *Klug 160* (F! NY! US!) as *S. puberum*. Examination of the Amazonian sericeous-leaved species of *Stigmaphyllon* and comparison with Jussieu's type revealed the distinctive species to which the name *S. cardiophyllum* applies.

Stigmaphyllon convolvulifolium Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840.—TYPE: FRENCH GUIANA. Cayenne, *Martin s.n.* (lectotype, designated by C. Anderson, 1987: P!).

Stigmaphyllon latifolium Bentham, London J. Bot. 7: 128. 1848.—TYPE: SURINAME. *Hostmann 146* (holotype: K-herb. Bentham!, photo: MICH!; isotypes: BM! G! K-herb. Hooker! NY-fragment! P! U! W!).

Vine to 15 m. Laminas 5–15 cm long, 4.5–11.5 cm wide, ovate to cordate or narrowly so, apex acuminate-mucronate, base cordate, very sparsely sericeous to soon glabrate or glabrous above, very sparsely and minutely sericeous (appearing glabrous to the naked eye) to glabrate to glabrous below [trabecula 0.1 (–0.2) mm long, straight, sessile], margin with irregularly spaced sessile glands (0.2–0.5 mm in diameter) and filiform glands (up to 1.6 mm long), with a pair of prominent but sessile glands at the base borne halfway on the petiole, each gland 1.1–2.6 mm in diameter; petioles 1.5–10 cm long; stipules 0.3–0.9 mm long, 0.5–1.3 mm wide, eglandular. Flowers ca. 15–40 per pseudoraceme, these borne in dichasia or compound dichasia or small thyrses. Peduncles 4–12.5 mm long, pedicels 3–9 mm

long; peduncles 0.7–2 times as long as the pedicels. Bracts 1–1.7 mm long, 0.8–1.2 mm wide, triangular; bracteoles 1–1.5 mm long, 0.7–1.3 mm wide, oblong to ovate, eglandular or each bracteole with a pair of inconspicuous glands (each 0.2–0.4 mm in diameter). Sepals 1.8–2.5 mm long and wide, glands 1.2–1.9 mm long, 0.7–1.2 mm wide. All petals with the limbs orbicular, glabrous, suffused with red, margin erose to denticulate-fimbriate, the teeth/fimbriae up to 0.2 mm long; anterior-lateral petals: claw (1.5–) 2–2.2 mm long, limb 11–12 mm long and wide; posterior-lateral petals: claw 1–1.5 (–1.7) mm long, limb 8–10 (–11) mm long and wide; posterior petal: claw (3.2–) 2.5–3.5 mm long, apex indented, limb 6–8.5 mm long and wide. Stamens unequal, those opposite the posterior styles the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced or rarely with only 1 reduced locule or eloculate; anthers usually all loculate, glabrous. Anterior style 2.8–3.3 mm long, shorter than the posterior two, with scattered hairs in the proximal 1/3–1/2; apex 1.5–1.9 mm long sometimes including a spur ca. 0.2 mm long; folioles variable, the larger folioles 0.9–1.5 mm long, 0.7–1.5 mm wide, parabolic to broadly lunate to subrectangular, sometimes much smaller, ca. 0.6 mm long, ca. 1 mm wide, broadly triangular. Posterior styles 3.1–4 mm long, with scattered hairs in the proximal 1/4–3/4, lyrate; foliole 1.5–1.8 mm long, 1.6–2 mm wide, suborbicular to subsquare to trapezoidal. Dorsal wing of samara 3.4–4.2 cm long, 1.2–2 cm wide, upper margin with a blunt tooth; nut bearing a pair of rectangular to semicircular to lunate, entire to grossly dentate lateral winglets, these 3.5–6.5 mm long, 1.2–2 mm wide, and often also with a few spurs and crests up to 1.5 mm long and 1 mm wide; nut 4.5–6.7 mm high, 3.5–4.3 mm in diameter, areole 3.3–3.5 mm long, 2.8–3.5 mm wide, concave, carpophore up to 3 mm long. Embryo 6–6.7 mm long, ca. 2 times as long as wide, ovoid, outer cotyledon 9–10.2 mm long, ca. 3.3 mm wide, the distal 1/3 folded over the inner cotyledon, inner cotyledon 6.6–7.3 mm long, 2.8–3.1 mm wide, folded at the distal 1/4–1/3.

Phenology. Collected in flower and fruit throughout the year.

Distribution. In moist forest, along rivers, and also in secondary growth and along roadsides; Guyana, Suriname, French Guiana, and northeastern Brazil (Amapá and eastern Pará), also recorded from Martinique and Trinidad; sea level to 300 m.

Representative Specimens. **Martinique.** Marigot, Ste. Marie, *Duss 1473* (NY); *Terrasson s.n.* in 1796 (P-JU). **Trinidad.** Maracas, *Broadway 8052* (A, BM, MO, S); NE of Point Fortin, *Davidse 2578* (F, GH, MO, NY).

Guyana. Northwest distr., Waini River, Marabo Creek, *de la Cruz 1267* (NY, US); Pomeroon dist., Pomeroon River, *de la Cruz 3044* (CM, F, GH, MO, NY, US); Kamakusa, upper Mazaruni River, ca. 59°50'W, *de la Cruz 4149* (CM, F, GH, NY, US); margins of Berbice River, S of New Dageraad, ca. 06°N, 57°43'W, *Maas et al. 5543* (MICH); Essequibo, *Meyer s.n.* (GOET). **Suriname.** Fluv. Coppename, Boon 1048, *1104* (U); Wilhelmina Gebergte, Lucie River, 03°20'N, 56°49'W, *Irwin et al. 55408* (F, K, MICH, NY, U, US), *Irwin et al. 55463* (C, F, K, MICH, MO, NY, RB, U); Paramaribo, *Kramer & Hekking 2338* (U); ad ripas fluv. Marowijne, *Lanjouw & Lindeman 2962* (NY, U); Jandé kreek, boven Suriname rivier, 1 1/2 uur varen beneden Kabel, *Lindeman 4455* (MO, U); Jodensavanne-Mapane kreek area, Suriname River, *Lindeman 5001* (U); Perica River, *Lindeman 5440* (COL, MICH); Saramacca River, rear of village Jacob kondre, *Maguire 23847* (F, GH, K, MO, NY, RB, U, US); fluv. Gonini, *Versteg 47* (U). **French Guiana.** Haut. Riv. Mana, amont de Sant Ananas, *Cremers 7531* (CAY, MICH); S de St. Jean du Maroni, *Cremers 7672* (CAY, MICH); route de St. Laurent á Paul Isnard entre les PK 10 et 40, *Cremers 7979* (CAY, MICH); fleuve Tampoc, á 4 km en amont de son confluent avec l'Ouaqui, *Granville B4834* (MICH, P); RN2, á proximité du pont sur l'Orapu, *Granville 5036* (CAY, MICH); Crique Cabaret-Bassin de l'Oyapock, entre l'embouchure et la crique Mérignan, 03°55'N, 51°48'W, *Granville 10235* (MICH); Trois Sauts,

Akattis Alasuka, *Haxaire 566* (CAY); Comté, entre Rodre Fondé et Belizón, *Oldeman 1449* (MICH); Haut Oyapock, environ 2500 avant l'embouchure de la rivière Eurupoucigne, *Oldeman B3289* (MICH); entre Cabassou et Degrad des Cannes, Île de Cayenne, *Prévost 1257* (CAY, MICH); rivière Inini, affluent du Moyen-Maroni (Lawa), en amont de Maripasoula, *Sastre et al. 3996* (CAY, MICH, P); Sinnamary, route de Ste. Elie, Km 17, *Sastre et al. 4199* (MICH, P); fleuve Approuague, près de Régina, *Sastre 4813* (CAY, MICH); montagnes de Kaw, auberge de Brousse des Cascades, 04°35'N, 52°17'W, *Weitzman 272* (MICH). **Brazil.** PARÁ: Obidos, Rio Paru de Oeste, *Cavalcante 801* (MG); Gurupá, Rio Amazon, *Killip & Smith 30594* (NY); Jari, estrada do Munguba, *N. T. Silva 2138* (IAN, MICH).—AMAPÁ: Rio Amapari, Serra do Navio, *Cowan 38206* (MICH, NY); Rio Jari, 0.5–3 km S of Santo Antonio da Cachoeira, 00°55'S, 52°55'W, *Egler & Irwin 46066* (MICH, NY, UB); confluence of Rio Iane with Rio Oiapoque, 02°53'N, 52°22'W, *Egler & Pires 47771* (MICH, NY); Mpio. Mazagão, BR-156, 81 km WSW of Macapá, ca. 11 km SW of Rio Preto, 00°08'S, 51°48'W, *Mori & Cardoso 17432* (MICH); Mpio. Calçoene, BR-156, 53–72 km WSW of Calçoene, ca. 02°33–38'N, 51°16'W, *Rabelo et al. 2964* (MICH); Rio Araguari, between 01°02'N, 51°45'W and 00°57'N, 51°29'W, *Pires et al. 50907* (IAN, MG, MICH, NY); between Rios Cujubim and Flechal, 01°45'N, 50°58'W, *Pires & Cavalcante 52435* (IAN, MG, MICH, NY).

Stigmaphyllon convolvulifolium is distinguished by its ovate to cordate leaves, whose lower surfaces are glabrate to glabrous but often very sparsely and minutely sericeous below (appearing glabrous to the naked eye); the sessile hairs are only 0.1 (–0.2) mm long. Only the stamens opposite the anterior-lateral sepals have enlarged connectives and reduced locules, and the styles are pubescent in the basal 1/4–3/4. The petals, especially the flag, are usually suffused with red. This species is most likely to be confused with the widely distributed and extremely variable *S. sinuatum* and in eastern Brazil (Pará) with *S. cardiophyllum* (see that species); *S. convolvulifolium* and *S. argenteum* are not sympatric. *Stigmaphyllon convolvulifolium* and *S. sinuatum* are similar in many aspects but can always be separated by the nature of the pubescence on the abaxial leaf surface. In the range of *S. convolvulifolium*, the common form of *S. sinuatum* has the leaves densely silver-sericeous below. A variant in French Guiana and in Amazonian Brazil has the leaves less abundantly pubescent abaxially though never as sparsely as in *S. convolvulifolium*; the hairs are (0.2–) 0.3–0.5 (–0.7) mm long.

The epithet "convolvulifolium" is often ascribed to Cavanilles, who published *Banisteria convolvulifolia* in 1790; however, Cavanilles cited Linnaeus's earlier *Banisteria dichotoma* [=*Stigmaphyllon dichotomum* (L.) Griseb.] in synonymy. Jussieu (1840) intended to make the combination in *Stigmaphyllon*, but because Cavanilles's name was superfluous, the name *Stigmaphyllon convolvulifolium* dates from Jussieu's publication. The lectotype is a Martin collection, annotated by Jussieu, that matches Jussieu's description.

Stigmaphyllon sinuatum (DC.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 288. 1840. *Banisteria sinuata* DC., Prodr. 1: 588. 1824. *Stigmaphyllon hastatum* var. β *sinuatum* (DC.) Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 24. 1900. *Stigmaphyllon sagittatum* var. β *sinuatum* (DC.) Nied., Pflanzenreich IV. 141(2): 506. 1928.—TYPE: FRENCH GUIANA. *Perrottet s.n.* (holotype: G-DC!, microfiche: MICH!, photos: F! GH! MICH! NY!). Fig. 3.

Banisteria heterophylla Willdenow, Sp. pl. 2: 742. 1799, non *Stigmaphyllon heterophyllum* Hooker, 1843. *Banisteria splendens* DC., Prodr. 1: 588. 1824, nom. superfl. *Stigmaphyllon fulgens* Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840, nom. superfl. *Stigmaphyllon splendens* Cuatr., Webbia 13: 531. 1958, nom. superfl.—TYPE: VENEZUELA. "ad Orinocum," *Bredemeyer s.n.* (holotype: B-W 8855, microfiche: MICH!).

Stigmaphyllon martianum Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840.—TYPE: BRAZIL. Amazônas: "in sylvis Japurensibus," Dec, *Martius s.n.* (holotype: M!, photos: F! GH! MICH! NY!).

Stigmaphyllon richardianum Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840.—TYPE: FRENCH GUIANA. Cayenne, July, *Richard s.n.* (holotype: P!, fragment: P-JU!, photos: F! MICH!).

Stigmaphyllon hypoleucum Miquel, Linnaea 18: 51. 1844.—TYPE: SURINAME. "ad fluv. Boven Cottica, in sylva," Oct 1842, *Focke 683* (holotype: U!).

Stigmaphyllon purpureum Bentham, London J. Bot. 7: 128. 1848.—TYPE: GUYANA. Picarara, *Robt. Schomburgk, 1st coll. 737* (holotype: K!, photo: MICH!; isotypes: G! P! W!).

Stigmaphyllon brachiatum Triana & Planchon, Fl. Novo-Gran. in Ann. Sci. Soc. Nat. Bot., sér. 4, 18: 316. 1842.—TYPE: COLOMBIA. Meta: Villavicencio, 450 m, *Triana s.n.* (holotype: P!, photos: F! GH! MICH! MO!; isotypes: COL! G!).

Stigmaphyllon monancistrum Niedenzu, Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 9. 1899.—TYPE: "Colombia" [VENEZUELA]. Aragua: Maracay, ad rivulis in crepidis, *Moritz 779* (lectotype, here designated: LE!; fragment of B duplicate: NY!).

Vine to 30 m. Laminas 6–21 cm long, 4.5–20 cm wide, triangular to ovate to cordate to elliptical to broadly so to orbicular to oblate to reniform, apex mucronate to emarginate-mucronate to short-acuminate, base acute to truncate to cordate to deeply auriculate, very sparsely sericeous to glabrous above, sparsely sericeous to densely silver-sericeous below [trabecula (0.2–) 0.3–0.5 (–0.7) mm long, straight, mostly sessile but sometimes with a tiny stalk up to 0.1 mm long, especially if vesture is very dense], margin grossly and shallowly crenate to subentire and with irregularly spaced sessile glands (0.4–1.5 mm in diameter) at the sinuses and sometimes also with filiform glands (up to 1.5 mm long), with a pair of prominent but sessile glands at the apex of the petiole, each gland 1–3.5 mm in diameter; petioles 1.8–13 cm long; stipules 0.5–1.3 mm long, 0.5–1.5 mm wide, eglandular. Flowers ca. 15–35 (–40) per pseudoraceme, these sometimes interrupted, borne in compound dichasia or small thyrses. Peduncles 1.5–11 mm long, pedicels 3–9.5 mm long; peduncles 0.4–1.5 times as long as the pedicels. Bracts 0.7–2 mm long, 0.5–1.4 mm wide, triangular or narrowly so; bracteoles 0.9–1.6 mm long, 0.7–1.3 mm wide, triangular to parabolic to ovate, eglandular or more commonly each bracteole with a pair of inconspicuous glands (each 0.1–0.5 mm in diameter) or sometimes only with a glandular area in the basal 1/3–1/2. Sepals 1.5–2.5 (–3) mm long, 1.5–2.5 (–3) mm wide, glands (1–) 1.2–2.2 mm long, 0.8–1.3 mm wide. All petals glabrous or sometimes pubescent abaxially, yellow or suffused with red, margin erose to erose-denticulate to denticulate, teeth up to 0.3 mm long, lateral petals with the limbs orbicular; anterior-lateral petals: claw (1–) 1.5–2.5 mm long, limb (8–) 10–15 mm long and wide; posterior-lateral petals: claw (0.5–) 0.8–2 mm long, limb (7–) 9–13 mm long and wide; posterior petal: claw 2.6–3.5 (–4) mm long, apex indented, limb (5–) 7–11 mm long and wide, broadly elliptical to broadly obovate to orbicular. Stamens unequal, those opposite the anterior style and/or the posterior styles the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced or sometimes with only 1 locule or rarely eloculate; anthers glabrous. Anterior style (2.6–) 3.2–4 (–4.8)

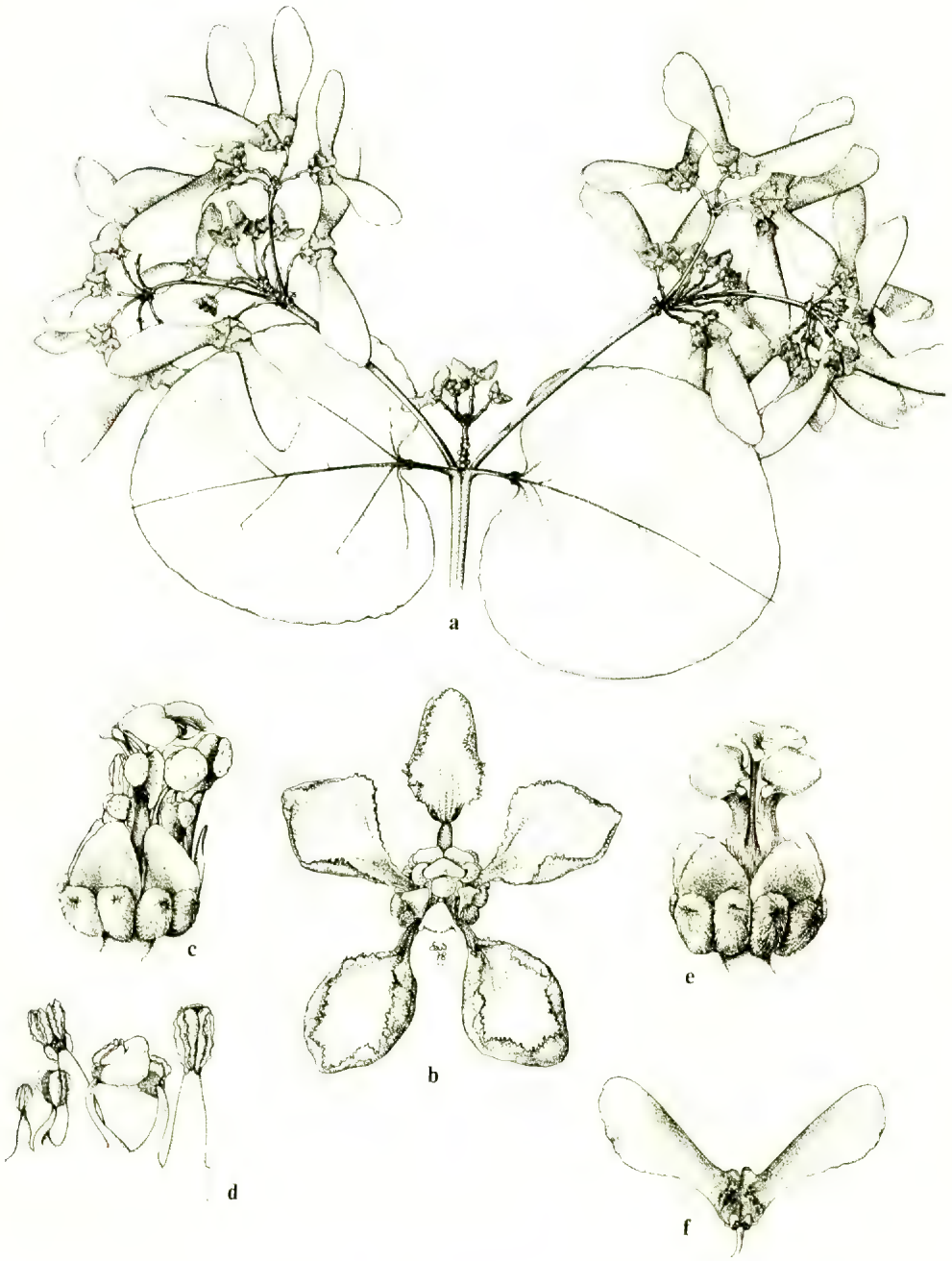

FIG. 3. *Stigmaphyllon sinuatum*. a. Fruiting branch (×0.5). b. Flower (×2.5). c. Flower with petals removed (×5); anterior sepal at right. d. Portion of androecium (×5); stamen at left opposite posterior petal. e. Flower with petals and androecium removed (×5); anterior style in center. f. Fruit with two samaras (×0.75). (Based on *Wurdack 34434*.)

mm long, shorter than or subequal to the posterior two, glabrous or commonly with a row of hairs adaxially in the proximal 1/5–2/3; apex (1.1–) 1.4–2.6 mm long, often including a spur 0.1–0.5 mm long, each foliole 0.7–1.9 mm long, 0.6–1.9 (–2.1) mm wide, triangular to parabolic to subrectangular *or* folioles absent and the apex extended into a claw 0.7–1.3 mm long. Posterior styles (2.8–) 3–4.5 (–5.2) mm long, glabrous or commonly with a row of hairs adaxially in the proximal 1/4–1/2, lyrate; foliole 1–2.2 mm long, (0.8–) 1.2–2.3 mm wide, subsquare to suborbicular or sometimes parabolic or rectangular. Dorsal wing of samara 3.5–5.5 cm long, 1–1.8 cm wide, upper margin with a blunt tooth; nut smooth or bearing 1–3 subentire to coarsely toothed to lacerate lateral winglets, these up to 6 mm long and 3.5 mm wide, and/or spurs and crests up to ca. 2 mm long and wide; nut 4.5–7 mm high, 2.8–4.4 mm in diameter, areole 2.3–4 mm long, 2.5–4.5 mm wide, concave, carpophore up to 5 mm long. Embryo 5.1–6.8 mm long, ca. 1.5–2 times as long as wide, ovoid, outer cotyledon (4.7–) 5.4–8.5 mm long, 2.5–4.2 mm wide, straight or the distal 1/5–3/5 folded over the inner cotyledon, inner cotyledon 4–6.3 mm long, 2.2–4 mm wide, straight or folded at the distal 1/4–2/3.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Common in the lowlands of Colombia, Venezuela, the Guianas, northern Brazil, Ecuador, northern Peru, and Amazonian Bolivia; in primary and secondary forest, especially wet forest but also in white sand vegetation, along rivers, at roadsides, in thickets; sea level to 1000 m.

Representative Specimens (anterior style foliolate). **Colombia**: Amazonas: ca. 6 km W of Leticia at Santa Isabella, 04°10'S, 69°58'W, *Gillett & Dickenson 16521* (COL, MO); Araracuara, near Río Caquetá, *Maguire et al. 44142* (MICH, NY); Leticia, ca. 1 km NE of town, *Plowman et al. 2291* (ECON, F, GH, NY); Leticia, *Schultes 8222* (COL, GH). **Venezuela.** Amazonas: Dept. Río Negro, along Río Marawinuma, vicinity of Cerro de la Neblina base camp, ca. 00°50'N, 66°09'W, *Liesner 15966* (MICH), *Nee 30880* (MICH); Tamatama, *Ll. Williams 15217* (F, NY, US), *Wurdack & Adderley 43641* (F, MICH, NY, U).—Anzoátegui: along Río Querecual, SW of Bergantín, *Steyermark 61506* (F, NY, VEN).—Aragua: Rancho Grande, *Badillo 1793* (MY).—Barinas: Allamira, *Curran M-619* (NY).—Bolívar: NE de Canaima, S de Cerro Venado, ca. 06°16'N, 62°46'W, *Agostini 299* (US); Ciudad Bolívar, Maquanta River, ca. 08°10'N, *Bailey & Bailey 1411* (A, NY); Calzeta en la Botella, Río Cuyuní, *Bernardi 6497* (MER, NY); a 48 km NE del caserio Los Rosos, este último a 17 km de Upata, sobre la carretera nueva Upata-San Félix, *Blanco 434* (MER, MO, NY, US); dist. Cedeño, 6 km from Maniapure toward Caicara, 06°55'N, 66°30'W, *Boom & Grillo 6487* (MICH); Mpio. Raúl León, Río Paragua, 04°18'N, 62°05'W, *Delgado 104* (MICH); Km 105–112 de la carretera El Dorado-Sta. Elena, *Morillo et al. 2932* (MICH); Mpio. Piar, camino desde El Plomo a Sta. Barbara, 06°45'30"N, 62°48'W, *Picón Nava 1588* (MICH); Uruyén, Auyantepui, *Schnee 1437* (MY); alrededores de Tumeremo, camino Tumeremo-Bochinche, entre Puesto (GN) Corumo y Caño Matuco del Río Negro, *Stergios et al. 3563* (MICH); Sierra Imataca, along Río Reforma, 1 km above junction with Río Toro, *Steyermark 87917* (MICH, NY, U, US); acercandose a las cabeceras del Río Nichare (affluente del Río Caura) en la dirección de la Sierra Maignalida y Sierra Cervatana, arriba de la desembocadura con el Río Cicuta (Icuta), 06°15'N, 65°05'W, *Steyermark & Gibson 95736* (NY, US); La Prisión, Medio Caura, *Ll. Williams 11539a* (F); El Palmar, *Ll. Williams 12919* (A, F, K, S); along Fundación rd, *Wurdack 34434* (NY).—Delta Amacuro: near border (=Río Grande o Toro) between Estado Bolívar and Terr. Delta Amacuro, ca. 08°04'N, 61°44'W, *Breteler 3757* (MER, VEN, NY, U, US); Depto. Tucupita, ca. 13 km by rd ESE of the town of Sierra Imata, 08°32'N, 62°23'W, *Davidse & González 16623* (MICH, MO); downstream from San Victor, Río Amacuro, Sierra Imataca, *Steyermark 87299* (G, NY, P).—Miranda: dist. Paez, Cerro Riberón between Río Guapo and Río Chiquito, 44.5 km (str. line) SE of Caucagua, 10°05'N, 66°01'W, *Davidse & González 13604* (VEN); between La Cortada and Turumo Bridge, *Pittier 11484* (G, K, NY, US, VEN); Los Mariches, *Pittier 12991* (F, G, M, MO, NY, US, VEN); Cerros del Bachilla, between Quebradas Corozal and Santa Cruz, S of Santa Cruz, 10 km by air W of Cúpira, *Steyermark & Davidse 116443* (MICH, MO).—Monagas: ca. 8 km ESE of Jusepín, *Pursell et al. 9098* (NY, US, VEN).—Sucre: Río Tatracual, 25 km outside Cumaná on Cumanacoa rd, *Sobel & Strudwick 2274* (MICH). **Guyana.**

Near Mazaruni Forest Station, *Archer 2463* (GH, K, US); Pomeroon Dist., Waramuri Mission, Moruka River, *de la Cruz 2578* (GH, NY, US); Waini River, NW Dist., 08°20'N, 59°40'W, *de la Cruz 3619* (F, GH, MO, NY, US); upper Demerara-Berbice region, ca. 27 km from Ituni along Ituni-Kwakwanni rd, 05°22'N, 58°07'W, *Gillespie 2991* (MICH); Potaro-Siparuni region, trail from Kato to Paramakatoi, 04°41'N, 59°50'W, *Hahn 5622* (MICH); Akyma, Demerara River above Wismar, 05°09'N, *Hitchcock 17414* (GH, NY, US, S); Kanuku Mts, Rupununi River, near "the farm" of the Captain of Sandcreek, 03°07'N, 59°26'W, *Jansen-Jacobs et al. 206* (MICH); Gunn's, Essequibo River, 01°39'N, 56°38'W, *Jansen-Jacobs et al. 1516* (MICH); Potaro-Siparuni region, Chenapou, 50 km upstream from Kaieteur Falls, 05°00'N, 59°34'W, *Kvist 325* (MICH); Cuyuni-Mazaruni region, NW of Conoch Tipu, 05°48'N, 61°03'W, *McDowell 2629* (MICH); Cuyuni River, by portage rd near lower Camaria Landing, *Sandwith 664* (K, NY, U); Essequibo River, near mouth of Orono Creek, ca. 01°35'N, *A. C. Smith 2821* (A, F, G, K, MO, NY, P, S, U); W extremity of Kanuku Mts, drainage of Takutu River, *A. C. Smith 3166* (F, G, K, MO, NY, P, S, U, W); ca. 5 km SW of Mabura Hill towards Essequibo River, 05°19'N, 58°38'W, *Stoffers et al. 35* (MICH); Marudi Mts, Mazoa Hill, near NorMan Mines camp, 02°15'N, 59°10'W, *Stoffers et al. 207* (MICH). **Suriname**. Scotelweg, *Archer 2658* (US); Zandrij, *Archer 2761* (US); Republieck, *van Doesburg, Jr., 70* (U); dist. Saramacca, Experimental Farm Coebiti, *Everaarts 519* (MICH); in montibus Bakhuis inter flum. Kabalebo et Coppename sinistrum, around Kabalebo airstrip, *Florschütz & Maas 2502* (F, U); dist. Nickerie, area of Kabalebo Dam project, ca. 22 km SW of Avanavero damsite, *Heyde & Lindeman 103* (MICH, U); without locality, *Hostmann 1029* (BM, G, GH, P, U, W); Wilhelmina Gebergte, Zuid River, 45 km above confluence with Lucie River, 03°10–20'N, 56°29–49'W, *Irwin et al. 57631* (K, MG, MICH, NY, S, U, US); Suriname River near Kabelstation, *Lanjouw 11185* (U); Nickerie Dist., area of Kabalebo Dam project, 04–05°N, 57°30'–58°W, *Lindeman et al. 47* (U); Lely Mts, SW plateaus, *Lindeman et al. 266* (NY, U); Waijombo River, *Linder 89* (GH, NY); vicinity of Sectie O, KM 68, *Maguire & Stahel 25000* (BR, F, G, GH, K, MO, NY, P, RB, U); Brownsberg Nature Park, 90 km S of Paramaribo, Mazaroni plateau, trail to Witti-creek, *Mori & Bolten 8397* (MICH, NY); surroundings of Blakawatra, camp 8, 60 km SE of Paramaribo, *den Outer 872* (U); fluv. Saramacca inf. prope Mindrinetti, *Pulle 34* (U); Jodensavanne-Mapanekreek area (Surinam R.), *Schulz 7313* (AAU, COL, MICH, NY, U, US). **French Guiana.** Sinnamary, piste de Ste. Elie, Km 15, *Billiet & Jadin 1101* (BM, BR, CAY, NY); piste Saint Laurent vers Paul Isnard, entre Km 30 et 40, *Billiet & Jadin 1577* (CAY, MICH); piste forestière allant de la route N2 vers Nancibo, *Billiet & Jadin 1845* (CAY); le long de la piste de la route de Cayenne á Régina, ca. 30 km de Régina, *Cremers 5991* (MICH); Bourg d'Apatou, Bassin du Maroni, 05°09'N, 54°20'W, *Fleury 334* (MICH); Haut Oyapock, Trois Sauts, *Garnier 103* (CAY); Haut Oyapock, á 2 km env. en amont de Saut Boko, *Granville 2465* (NY); Haute Camopi, Mont Belvédère, *Granville 7010* (CAY, MICH); roche plate Roche Koouton-Bassin Haut-Marounini, 1 km W de la Roche, 02°53'N, 54°04'W, *Granville 9516* (MICH); St. Georges de l'Oyapock, piste de Maripa, *Grenand 2136* (CAY, MICH); Île de Cayenne, Mont Bachrel, 04°55'N, 52°19'W, *Hoff 5224* (MICH, P); village de Zidockville, Trois Sauts, *Jacquemin 1610* (CAY, MICH); Saül, 03°37'N, 53°12'W, *Marshall & Rombold 169* (CAY, MICH); Maripasoula, *Oldeman 1647* (MICH); rivière Tonégrande, près de port Inini, *Oldeman 1656* (MICH, P); Saül, *Oldeman 1982* (CAY, MICH, P); fleuve Approuague, rivière Arataye, Sauts Pararé, *Poncy 221* (CAY); Acarouani, *Sagot 91* (BM, G, P, S, W); St. Laurent region, ca. 5 km from Rte D9 at Charvein, 05°51'N, 53°51'W, *Skog & Feuillet 7481* (CAY, NY, P); main rd through Montagne de Kaw, 04°35'N, 52°15'W, *Weitzman 308* (MICH). **Brazil.** Acre: Cruzeiro do Sul, Projecto RADAM/BRASIL, aeroporto, *Monteiro & Damião 209* (INPA, MG), *Ramos 116* (INPA), *Ramos & Mota 208* (INPA); near Sta. Lucia, Km 40 on Transamazônica Hwy, E of Cruzeiro do Sul, 07°08'N, 72°33'W, *Pruski 3498* (MICH).—Amapá: 2–10 km N de Ferreira Gomes, BR-156, *Austin 7257* (MICH); Rio Amapari, rd to Porto Terezinha, *Cowan 38466* (K, NY, RB), *Cowan 38473B* (NY); Rio Amapá, Serra do Navio, lower slopes of Fritz Akerman Ore Body, *Cowan & Maguire 38086* (COL, G, GH, MICH, MO, NY, P, S, U, W); Rio Oiapoque, 6 km SE of Clevelandia, 03°48'N, 51°53'W, *Irwin et al. 47382* (IAN, MICH, NY); Mpio. Oiapoque, BR-156, 60 km SSE of Oiapoque, 03°18'N, 51°39'W, *Mori & Cardoso 17134* (MICH); Macapá, Igarapé do Lago, *Rabelo & Non 771* (MG); Matapi, *Ribeiro 1597* (INPA, MICH, MO, NY, RB).—Amazônas: Mpio. Tefé, Rio Solimões, vila Nogueira, *Amaral et al. 95* (INPA, NY); Manaus-Pôrto Velho hwy, Km 124, *Campbell et al. P20920* (INPA, MICH, MO, NY, S, U); Manaus, Igarapé do Parque 10, *Chagas INPA 3679* (INPA, SP); Rio Uatumã, Mpio. Itapiranga, *Cid et al. 592* (INPA, MICH); BR-172, Manaus-Caracaraí, Km 97, *Cid et al. 945* (INPA, MICH); Mpio. Maraã, Rio Japurá, affluente do Rio Solimões, *Cid & Lima 3434* (INPA, MG, MICH); BR-307, Mpio. Cruzeiro do Sul, 7–8°S, 72–73°W, *Cid Ferreira et al. 5218* (INPA, MICH); Mpio. São Paulo de Olivença, 6 km S of town center, 03°30'S. 68°57'W, *Daly et al. 4442* (MICH); Barcelos, *Duarte 7160* (INPA, RB, SP); Manaus, estrada do Mindú, *Ducke 856* (F, IAN, MG, MO, NY, R, RB, US); Mpio. Maués, ca. 20 km E of Maués, Antarctica Guaraná Planta-

tion, *Hill et al. 13152* (JBSD, MICH, TEX); Manaus, Rua Duque de Caxias, *Maas & Maas 362* (INPA, U); caatinga do Porto Camanaus, *Madison et al. PFE 414* (INPA); basin of Rio Demeni, vicinity of Tototobí, *Prance et al. 10355* (INPA, MG, MICH, NY, U); Manaus, INPA, estrada do Aleixa, Km 3, *Prance & Ramos 20922* (INPA, MICH, MO, NY, U); vic. of Pico Rondon, Perimental Norte, Km 211–220, 01°32'N, 62°48'W, *Prance et al. 28821* (MICH), *Rodrigues et al. 10584* (MICH); Santo Antonio do Içа, p. Vila Militar, *M. Silva 2112* (MG); Fonte Boa, *M. Silva 2183* (MG); Barra [=Manaus], *Spruce 1880* (G, GH, LE, M, MG); Mpio. Humaitá, estrada Humaitá-Lábrea, Km 59, a 3 km ao N, *Teixeira et al. 980* (INPA, MICH); Mpio. Humaitá, estrada Humaitá-Jacarecanga, Km 150, a 63 km ao S, *Teixeira et al. 1340* (INPA, MICH).—Maranhão: Mpio. Monção, basin of the Rio Turiaçu, Káapor Indian Reserve, *Balée 886* (NY); ca. 50 km from Santa Luzia on Hwy to Açailândia, 04°05'S, 45°57'W, *Daly et al. D736* (MICH); Rio Alto Turiaçu, Barranquinha, 03°00'S, 45°45'W, *Jangoux & Bahia 161* (MG, NY); margen do Rio Cururupu, *Lisboa 47* (RB, SP); Km 375–380 da rodovia Belém-Brasília, *Oliveira 1072* (IAN, UB).—Pará: Belterra, *Black 47-1660* (IAN); Altamira, Km 74 da estrada Transamazônica Itaituba, *Cavalcante & M. Silva 2780* (MG); Mpio. Oriximiná, Rio Trombetas, Lago de Matens, 19 km S de Pôrto Trombetas, *Cid et al. 1793* (INPA, MG, MICH); Jacaracá Island, *da Costa 149* (F); ca. 70 km from Tucuruí, ca. 04°11'S, 49°04'W, *Daly et al. 1435* (INPA, MICH); boca do Lago de Faro, *Ducke 88677* (MG); 4–5 km W of São Francisco do Pará toward Castanhal, *Gentry 13166* (INPA, MICH, MO, NY); dist. Acará, Thomé Assú, Pau Vermelho, *Mexia 5926* (A, F, G, GB, GH, MICH, MO, NY, S, U, WIS); Belém, horta do IAN, *Murça Pires & Black 403* (GH); Mpio. Almeirim, Monte Dourado, estrada MTD, W em direção à mina de bauxita, *Murça Pires et al. 620* (MICH); BR-163, Km 1131, Ciuabá-Santarém highway, vicinity of Igarapé Natal, *Prance P25427* (MG, MICH); Belém, terreno da EMBRAPA, *Ramos & Rosário 14* (MG); Ourém, *Rodrigues 4024* (MG); Tucuruí, margem direita do Rio Tocantins, *Rosário 93* (MG, NY); Mpio. Almeirim, Monte Dourado, *Santos 437* (NY); Santarém, Km 70 da estrada do Palhão, arredores do Acampamento do Igarapé Guaraná, *M. Silva & R. Souza 2522* (MICH, NY, U), *M. Silva & R. Souza 2522* (CAS, CM, MG, MICH, NY); 7–11 km NW of AMZA camp 3-Alfa on rd to camp 4-Alfa, 05°47'S, 50°34'W, *Sperling 6057* (MICH); Santarém, *Spruce 767* (G, GH, GOET, M, NY, W); Macau airstrip, 1 1/2 hrs upstream from Lageira airstrip, 05°55'S, 54°26'W, *Strudwick & Sobel 3474* (MICH); Taperinha bei Santarém, *Zerny 589* (W).—Rondônia: Pôrto Velho-Cuiabá hwy, 25 km S of Nova Vida, *Forero & Wrigley 7084* (INPA, MG, MICH, NY); basin of the Rio Madeira, cerrado between Jaciparaná and Rio Madeira, *Prance et al. 5180* (INPA, MG, MICH, NY); Km 166–169, Madeira-Mamoré railroad near Mutumparaná, *Prance et al. 5690* (INPA, MG, MICH, NY); foothills of Serra dos Pacaás Novos, 12 km NNE of Guajará-Mirim, *Prance et al. 6658* (F, INPA, MICH, NY); Pôrto Velho-Cuiabá hwy, vicinity of Santa Barbara, 15 km E of Km 117, *Ramos & Prance 6905* (INPA, MICH, NY); Pôrto Velho, Represa Samuel, 08°55'S, 63°16'W, *Thomas et al. 4949, 5034* (MICH).—Roraima: Aritumã region, on an azimuth of 011° from Boa Vista at a distance of 210 km, *Coradin & Cordeiro 943* (INPA, MICH, NY); SEMA Ecological Reserve, Ilha de Maracá, 03°21'N, 61°27'W, *Milliken M792* (MICH); Canto Galo, Rio Mucajaí, between Pratinha and Rio Apiaú, *Prance et al. 3964* (INPA, MG, MICH, NY, U); Serra Tepequem, *Prance et al. 4437* (INPA, MG, MICH, NY, U); vicinity of Uaicá airstrip, Rio Uraricoeira, 03°33'N, 63°11'W, *Prance et al. 10909* (INPA, MG, MICH, NY, U); Mpio. Caracaraí, estrada Manaus-Caracaraí, Km 529–550, *dos Santos & Coêlho 700* (INPA, MICH); estrada Manaus-Caracaraí, BR-174, Km 329, army post N of Waimari-Atoari Indian Reserve, *Steward et al. 9* (MICH); Rio Surumu, an einem Bache der Serra do Mel, *Ule 8185* (MG). **Bolivia.** Beni: Vaca Diez, 3 km E of Riberalta on rd to Guayaramerín, 11°00'S, 66°05'W, *Solomon 7682* (MICH). **Peru.** Huánuco: Prov. Leoncio Prado, Moena, cerca a Tingo María, *Woytkowski 1187* (MICH); Santa Tereza, valle del Huallaga, *Woytkowski 1232* (ECON).—Loreto: Prov. Coronel Portillo, Pampa de Sacramento, cerca Pucallpa, *Ferreyra H. 1184* (GH, MICH, US); Prov. Alto Amazonas, entre Yurimaguas y Chambira, *Ferreyra H. 4897* (MICH, US); Prov. Coronel Portillo, on Río Aguaytia, 08°50'S, 75°20'W, *Fosberg 28875* (MO); Balsapuerto, *Klug 3075* (A, BM, F, G, K, MO, NY, S, US); Prov. Ucayali, Canchahuayo (Río Ucayali), 07°05'S, 75°10'W, *Vásquez et al. 6970* (MO); Mariscal Castilla, Caballococha, 03°55'S, 70°30'W, *Vásquez & Jaramillo 9319* (MICH).—San Martín: ca. 10 km NE of Tarapoto, *Gentry et al. 37915* (MICH); San Martín, 5–15 km E of Shapaja on rd to Chazuta, 06°36'S, 76°10'W, *Knapp & Mallet 7026* (MICH); Prov. Mariscal Caceres, Dtto. Uchizo, en la carretera a Río Uchizo 2 km del caserio Nuevo Progreso, *Schunke V. 3219* (COL, F, G, NY, US); Prov. Mariscal Caceres, Dtto. Tocache Nuevo, Quebrada Luis Sálas (5 km NE de Puerto Pizana), *Schunke V. 6578* (GH, MO).

Representative Specimens (anterior style clawed). **Colombia.** Amazonas: Leticia, Oct 1946, *Black s.n.* (IAN); Río Iagara-Paraná (affl. Río Putumayo), La Chorrera, *Gasche & Desplats 59* (K, MICH).—Antioquia: Mpio. Caucasia, along rd to Nechí, 24 km from Caucasia-Planeta Rica rd, 08°04'N, 75°05'W, *Zarucchi et al. 4903* (MICH).—Caquetá: 6 km SE of Morelia along rd to Río Pescado (SW of Florencia), *Davidse 5644* (COL, MICH); Río Arteguaza, 9 km S of Florencia,

Plowman & Kennedy 2282 (F, GH, M, NY, P, S, US).—Meta: Villavicencio, *Killip 34346* (COL, S); Sierra de la Macarena, Río Guapaya, *Philipson et al. 2124* (COL).—Vaupés: rd from Mitu to Monfort, *Davis 107* (COL, GH, MICH). **Venezuela.** Amazonas: alrededores de San Juan de Manapiare, 05°18'N, 66°03'W, *Agostini 1504* (MICH); Río Orinoco, Isla del Ratón, 05°02'N, 67°45'W, *Breteler 4721* (F, K, MO, NY, US, WAG); Depto. Atures, 26 km SE de Puerto Ayacucho por la carretera Puerto Ayacucho-El Gavilán, 05°32'N, 67°24'W, *Cuello & Fernández 508* (MICH); El Gavilán, 30 km al E de Puerto Ayacucho, *Fernández 2950* (MY); Río Ventuari, La Ceiba, bajo del Salto Tencua, *Foldats 147A* (NY, VEN); Depto. Río Negro, cerca de Shabono Yanomami ubicado a la izquierda del Río Orinoco y a la derecha de la desembocadura del Río Mavaca, 02°30'N, 65°10'W, *Guanchez 656* (MICH); Cerro Camani, *Maguire 31802* (NY); ad flumina Casiquiari, Vasiva, et Pacimoni, *Spruce 3277* (BR, G, K, NY, W); Depto. Atabapo, Río Cunucunuma, entre el Cerro Duida y Huachamacari, 03°40'N, 65°45'W, *Steyermark et al. 126178* (MICH).—Araguas Pozo del Diablo, cañada del Río Yuare, Maracay, *Baldillo 3782* (F, MY); Rancho Grande, Maracay, *Ferrari 745* (MY), *Vogelsang E10* (MY).—Barinas: Ticoporo Forest Reserve, 08°15'N, 70°45'W, *Breteler 3678* (G, MER, NY, S, U, US, VEN); entre Km 469–470, carretera Barinas-San Cristóbal, *Cárdenas de Guevara et al. 2565* (MY); 1–2 km NE of Bumbum, ca. 68 km SW of Barinas, *Gentry et al. 11142* (MICH, MO, VEN).—Bolívar: Pica Caicara del Orinoco-San Juan de Manapiare, Río Suapure, 202 km al S de Caicara, ca. 07°N, 67°W, *Delascio & López 2766* (VEN); Santa María de Erebato, Río Erebato, 05°05'N, 64°40'W, *Steyermark et al. 109847* (K, NY).—Carabobo: Dtto. Valencia, carretera Valencia-El Palotal-El Paito-Los Naranjos, *Bunting 4597* (NY); Guataparo, Valencia, *Saer 865* (VEN).—Distrito Federal: Caracas, *Bredemeyer 206* (W); Depto. Vargas, camino entre Osma y Oritapo, *Benítez de Rojas 588* (MY).—Falcón: carretera Yaracal-Araurima, 8 km de la carretera Yaracal-Tucacas, *Cardozo et al. 65* (MICH); El Guanábano, 27 km S de Puerto Cumarebo, *Flora Falcón 343* (MICH, MO, U); Dtto. Silva, ca. 21 km W of Tucacas, *Wingfield 12696* (MICH).—Lara: Dtto. Palavecino, carretera entre Manzanito y El Altar, *Burandt, Jr., & Smith V0075* (MICH).—Mérida: above dam site on Río Caparo, 31 km ESE of Santa Barbara, ca. 07°41'N, 71°28'W, *Liesner & González 9267* (MICH, VEN).—Portuguesa: Dtto. Ospino, carretera La Aparición de Ospino-Moroturo, 09°31'N, 69°26'W, *Aymard & Cuello 6577* (MICH); Dtto. Araure, carretera Hoja Blanca-Guayabal-El Rechazo, *Cuello & Cuello 59* (MICH).—Táchira: E of San Cristóbal and 40 km W of Santa Barbara, rd W or NW of Abajales, *Sobel & Strudwick 2108* (NY).—Trujillo: Boconó, *López-Palacios 395* (MER, VEN).—Zulia: Dtto. Colón, hacienda El Rosario, 18 km E de la carretera Machiques-La Fría, 12 km N de Río Catatumbo, *Bunting 6475* (MICH, VEN); Dtto. Colón, entre Casigua El Cubo y Km 8 de la vía rumbo al Palmira, *Bunting 7328* (MICH); Dtto. Perija, entre Km 16 de la carretera Machiques-La Fría y Calle Larga y San José, *Bunting 10816* (MICH); Dtto. Perija, between Río Yasa and Río Tucuco along the Machiques and Los Angeles de Tucuco rd, 09°50–56'N, 72°40–44'W, *Davidse et al. 18390* (MICH). **Ecuador.** Morona-Santiago: Tunantza, Jíbaro settlement near Macuma, ca. 50 km NE of Macas, *Lugo S. 3718* (GB, MICH); El Centro Shuar Kankaim (Cangaime), Río Kankaim (Cangaime), 02°20'S, 77°41'W, *Shiki RBAE219* (NY).—Napo: carretera Hollín-Loreto-Coca, entre Avila y Río Pocuno, 00°39'S, 77°22'W, *Cerón et al. 2879* (MICH); Parque Nacional Yasuní, Pozo Petrolero "Cowi" de Conoco, 00°55'S, 76°20'W, *Coello 171* (MICH); Puerto Francisco de Orellana (Coca), ca. 40 km SE of town, Auca oil field, 00°42'S, 76°52'W, *Balslev & Madsen 10595* (AAU, MBM, MO, NY); near end of the Auca oil field rd, 00°44'S, 76°54'W, *Brandbyge & Asanza 30109* (AAU, MICH); rd Coca (Puerto Francisco de Orellana) to Curaray, ca. 40 km SE of Coca, *Harling et al. 14757* (GB, MICH); Dureno on Río Aguarico, *Harling & Andersson 16605* (GB, MICH); Río Auyabeno, near Puerto Montúfar, 00°06'S, 76°01'W, *Holm-Nielsen et al. 21281* (AAU); Río Aguarico, Monte Cristi, 00°18'S, 76°117'W, *Holm-Nielsen et al. 21666* (AAU); Estación Experimental de INIAP, San Carlos, 6 km SE de los Sachas, *Neill et al. 6216* (MICH); a 2 km de Jatun Sacha, en vía a Tena, 5 km de Misahuallí, 01°08'S, 77°30'W, *Palacios 2789* (MICH).—Pastaza: 31 km N of Puyo on rd to Tena, side rd E of Cajabamba, 00°15'S, 77°50'W, *Boom & Beardsley 8436* (MICH); Curaray (Jesús Pitishka), *Harling & Andersson 17450* (GB, MICH); Río Chullana, ca. 15 km N of Puerto Sarayacu, *Lugo S. 4184* (GB, MICH); Río Curiacu, ca. 8 km W of Puerto Sarayacu, *Lugo S. 4238* (GB, MICH); vicinity of El Porvenir, ca. 5 km W of Puyopunga, *Lugo S. 4942* (GB, MICH); trail to Copataza, 10 km S of Sarayacu, *Lugo S. 5519* (GB, MICH); carretera de Petro-Canada, vía Auca, 115 km S de Coca, 6 km S del Río Tiguino, *Zak & Rubio 4339* (MO). **Brazil.** Pará: Tucuruí, Ramos 1115 (INPA). **Peru.** Amazonas: valle del Río Santiago, ca. 65 km N de Pinglo, Quebrada Caterpiza, *Huashikat 1110* (MICH, MO); Prov. Bagua, 8 km E of Montenegro at Km 286 E of Olmos on the Mesones-Muro hwy, *Hutchison & Wright 3781* (F, GH, K, M, MICH, MO, NY, P, US); Mirana, *Woytkowski 5649* (G, GH, MO, US); Prov. Bagua, valley of the Río Marañón above Cascadas de Mayasi, Km 276–280 of Marañón rd, *Wurdack 1841* (F, NY, S, US).—Loreto: Maynas, Shusuna, carretera a Zungarococha, *Ayala 437* (AMAZ, MO); Río Yuvineto,

affluent du Río Putumayo, Río Putumayo, *Barrier 441* (AMAZ, MICH); cerca de Zúngaro, Cocha, 15 km SW de Iquitos, *Dodson 2809* (MO, SEL, US); Nauta, Río Marañón above mouth of Río Ucayali, 04°30'S, 73°30'W, *Gentry et al. 29968* (AMAZ, MICH); Maynas, Quebrada Sucursari, Río Napo, 03°15'S, 72°55'W, *Gentry et al. 42673* (MICH); Mishuyacu, near Iquitos, *Klug 113* (F, NY, US); Prov. Loreto, Pampa Hermosa and vicinity, Río Corrientes, 1 km S of junction with Río Macusarí, 03°15'S, 72°50'W, *Lewis et al. 10651* (MO); Maynas, Iquitos, Quista Cocha, *McDaniel 10907* (F, MO); Requena, Río Tepiche, Santa Elena, *McDaniel & Marcos 11263* (F, MO); Santa Ana on the Río Nanay, *Ll. Williams 1225* (F, US).

Stigmaphyllon sinuatum is a common and polymorphic species of the lowlands of northern South America to which several names have been applied. Its flowers are borne in pseudoracemes arranged in compound dichasia and thyrses with axes to the sixth order. The androecium differs from that of most species in that the posterior-lateral stamens bear unmodified anthers. Only the anterior-lateral stamens have the connective enlarged and the locules reduced; sometimes one or rarely both locules are absent. All anthers are glabrous. The styles are usually bearded adaxially but sometimes glabrous, and the posterior ones are always foliolate; the anterior style either bears two folioles or lacks them, or rarely is irregularly ornamented. The samara, like that of most species, has a large flaring dorsal wing, and the nut commonly bears on each side 1–3 lateral winglets and/or spurs and crests.

Stigmaphyllon sinuatum is highly variable in the shape and abaxial pubescence of the leaves, the color of the petals, and the presence of folioles on the anterior style. Representatives combining the various expressions of these characters have been segregated as species. Although the extremes are striking and may show some geographic correlation, they are linked by intermediates occurring throughout the range and thus are not accorded taxonomic recognition here. In Fig. 4, the various combinations of leaf pubescence and ornamentation of the anterior style are mapped; however, this map reflects more the itineraries of collectors than the range of the species.

The laminas vary from triangular to ovate to cordate to elliptical to orbicular to oblate to reniform, and are cordate to auriculate at the base to sometimes truncate or acute in smaller ones. In general, plants from the eastern and western part of the range have rather broad laminas (i.e., broadly elliptical to orbicular to oblate to reniform), and those from the central part are more likely to have triangular to ovate to elliptical ones. The appressed abaxial pubescence imparts a silvery metallic sheen. The abundance of the hairs varies greatly from sparse (the hairs barely if at all touching) to moderate (the hairs touching and/or overlapping but the epidermis visible) to so dense that the epidermis is hidden by a silver mat of hairs. The very dense pubescence is most common in plants from the eastern part of the range (Fig. 4).

The petals range from entirely yellow to yellow with varying amounts of red. If the petals in bud are yellow, they may remain yellow at maturity, or the flag and sometimes also the lateral petals may show red streaks. If the petals are red in bud, the expanded petals may be mostly red with only a yellow spot on the adaxial surface, may be mostly yellow but with a broad red band along the margin, or only the flag may be red and the lateral petals mostly yellow with a little red, either in streaks or along the margin. Sometimes the red pigment is evident only in bud and the expanding petals but is absent from the mature petals. Mostly, pure yellow limbs are slightly larger than those suffused with red. Specimens from Colombia, Ecuador, and Peru nearly always have yellow petals lacking red,

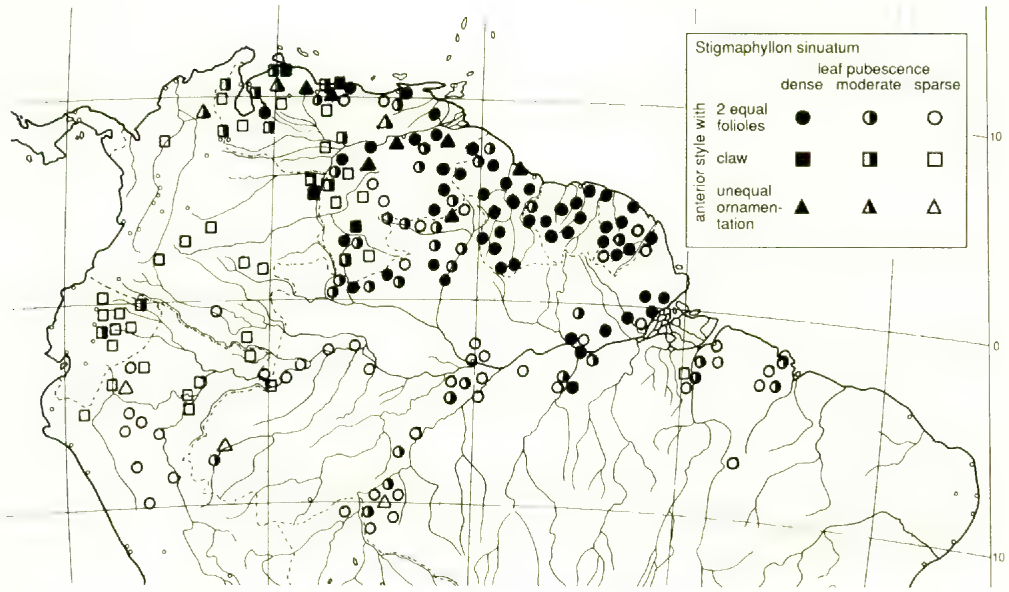

FIG. 4. Distribution of the variants in leaf pubescence and ornamentation of the anterior style of *Stigmaphyllon sinuatum*.

but yellow petals with minor red markings have also been reported (e.g., Ecuador: *Harling et al. 14757*; Colombia: *Davis 107*; Peru: *McDaniel 10907*). The petals are abaxially sericeous in nearly all collections from Amapá, Brazil, and rarely in specimens from other parts of the range (e.g., *Teixeira et al. 1340*, Amazônas, Brazil; *Murça Pires et al. 620*, Pará, Brazil; *Wurdack 34434*, Bolívar, Venezuela). Pubescent petals are otherwise known only in *S. singulare* C. Anderson, a very different species of Venezuela (Táchira) and Colombia (Norte de Santander).

The names *Banisteria heterophylla*, *B. splendens, Stigmaphyllon splendens*, *S. fulgens*, *S. hypoleucum*, and *S. purpureum* are based on collections from eastern Venezuela and the Guianas. The laminas of plants from the northeastern part of the range are usually orbicular to oblate or reniform and densely silver-sericeous below (Fig. 4, closed symbols). The petals have broad red-orange margins or may be entirely red with only a central yellow spot abaxially. The anterior style bears folioles.

In plants from the western part of the range as well as from the area of Belém (Pará), the Rio Tocantins and its tributaries, and Maranhão, all in Brazil, the laminas are most often broadly cordate to broadly ovate or sometimes narrower, though the orbicular to oblate/reniform shape is also infrequently encountered; the abaxial hairs are sparsely to moderately abundant (Fig. 4, open and partly closed symbols, respectively). Most commonly, the petals are yellow. The form with abaxially sparsely to moderately sericeous laminas and foliolate anterior styles is commonly assigned to *S. martianum*, a name based on a collection from Manaus (Amazônas, Brazil). The majority of specimens from the vicinity of Manaus, including the type of *S. martianum*, have triangular to ovate laminas that are acute to truncate to cordate at the base and sparsely sericeous below; the petals are yellow.

Much overlap occurs in the general ranges of the leaf variants. The laminas of plants of Guyana are often not quite as densely pubescent as those from French Guiana and Suriname. In a few collections from French Guiana, including the type of *S. richardianum*, the elliptical to broadly so to cordate (but not orbicular)

laminas are sparsely to moderately sericeous below, and the petals often lack red pigments (e.g., *Grenand 2136, Oldeman 1982, Jacquemin 1610*). A few collections of these variants are also known from Guyana (e.g., *de la Cruz 2578, Sandwith 664*), Suriname (e.g., *Lindeman et al. 47*), eastern Venezuela (e.g., *Sobel & Strudwick 2274*, Sucre), eastern Brazil (e.g., *Cowan 38473B, Irwin et al. 47382*, Amapá). Some collections from Manaus have yellow-red petals and very broad (suborbicular) though abaxially sparsely pubescent laminas (e.g., *Campbell et al. P20920, Maas & Maas 362, Chagas INPA 3679*). Most collections from the vicinity of Santarém have broad, abaxially densely sericeous laminas and red-yellow petals; yet, plants with sparsely to moderately pubescent laminas and yellow petals occur there as well (e.g., *Silva & Souza 2522*). In Roraima, the entire spectrum of variation in laminar shape and pubescence and in petal color is encountered. In some specimens from this region and elsewhere (e.g., *Prance 3964, 10909*, Roraima; *Thomas et al. 5034*, Rondônia), the abaxial surface of the young leaves and smaller ones near the inflorescence is densely sericeous, whereas that of the larger leaves is only moderately pubescent. The broad laminar shape and yellow-red petals typical of the eastern variant is also found in plants collected along the Rio Madeira (e.g., *Teixeira et al. 980, Prance et al. 5180*) and in northern Rondônia (e.g., *Prance et al. 6658, Thomas et al. 4949*) as well as along the Rio Mamoré and adjacent Bolivia (e.g., *Solomon 7682*); however, the laminas are only sparsely to moderately pubescent below. In most collections from Ecuador and Peru, the laminas also are broadly elliptical or cordate to orbicular.

In a few species of *Stigmaphyllon* characterized by foliolate anterior styles, individuals are occasionally encountered in which the folioles of the anterior style are greatly reduced or one or both are absent. Such atypical forms are known in *S. adenodon* Adr. Juss. (Peru), *S. lindenianum* Adr. Juss. (Yucatan Peninsula, Mexico), and *S. sagraeanum* Adr. Juss. (Cuba). In *S. sinuatum*, plants from the greater part of the range have foliolate anterior styles (Fig. 4, circles), but in many from western Venezuela (and also Amazonas and western Bolívar), Colombia, Ecuador, and northern Peru (Amazonas and Amazonian Loreto) the apex of the anterior style is efoliolate but extended into a claw 0.7–1.3 mm long (Fig. 4, squares). Exceptions to this geographical pattern are rare but not unknown; for example, in *Ramos 1115* from Tucuruí, Pará, Brazil, the anterior styles are efoliolate, and in *Maguire et al. 44142* from Araracuara, Amazonas, Colombia, they are foliolate. The names *Stigmaphyllon brachiatum* and *S. monancistrum* are based on the efoliolate form. In his treatment of *Stigmaphyllon* in the Guayana Highlands, W. R. Anderson (1981) commented on the morphological diversity of this species and questioned the validity of taxonomic recognition of the efoliolate variant as *S. brachiatum*.

Intermediate style forms occur, infrequently, throughout the range of *S. sinuatum* (Fig. 4, triangles). In these individuals, the anterior style may bear only one or two greatly reduced folioles, only one large foliole, or one reduced and one large foliole. The size and/or presence of such folioles may vary even within the same inflorescence or even the same umbel. Such intermediates otherwise share the characters of "normal" plants of their part of the geographic range. The following collections serve as examples of plants with variable anterior styles: Guyana, *Jenman 6875*, two large to tiny folioles; Suriname, *BBS 254, 259*, one foliole or two unequal folioles; Venezuela, *Trujillo 4127* (Aragua), *Pittier 5699, 12105, Diederichs 88* (Yaracuy), *Steyermark 61019* (Azoátegui), *Stergios 6224, 8902, Bernardi 7226* (Bolívar), all with one foliole or two unequal folioles; Colombia, *García B. 18248* (Norte de Santander), one foliole or two unequal folioles;

Brazil, *Maas P12815* (Acre), *Vieira et al. 546* (Rondônia), all with one foliole or two unequal folioles; Peru, *Huashikat 1375* (Amazonas), two folioles or one folio and a narrow lip. In one Venezuelan collection (*Romero 545*, Yaracuy), the anterior styles varies from hooked, i.e., without folioles, to bearing 1–2 large folioles. The absence or variability of folioles of the anterior style might indicate irregularities caused by hybridization; however, a preliminary survey of pollen showed no correlation between absence of folioles and presence of malformed pollen grains. In most samples of all three variants of ornamentation of the anterior style only few misshapen grains were found; the pollen was mostly 95–99% normal (at least 91% normal). The few exceptions are: *Oldeman 1982* (French Guiana, 86% normal), *Maguire 44142* (Colombia, Amazonas, 85% normal), *Prance et al. P25427* (Brazil, Pará, 58–72% normal), all three collections with foliolate anterior styles; and *Breteler 4721* (Venezuela, Amazonas, 83–84% normal), anterior styles efoliolate. Only in two collections did the pollen consist entirely of misshapen, thick-walled grains: *Broom & Beardsley 8436* (Ecuador, Pastaza, anterior styles efoliolate) and *Bernardi 7226* (Venezuela, Bolívar, anterior styles with variable folioles).

Because *S. sinuatum* is so variable and widespread, sympatric species with abaxially sericeous laminas have often been confused with it; for separation from these species, see the key presented above and the discussions of *S. argenteum*, *S. cardiophyllum*, and *S. convolvulifolium*.

In addition to taxonomic difficulties, *S. sinuatum* has also been a source of nomenclatural problems. The species was first described by Willdenow (1799) as *Banisteria heterophylla*. De Candolle (1824) considered this name unsuitable and in his *Prodromus* substituted the name *B. splendens*. Cuatrecasas (1958) published the name *Stigmaphyllon splendens*; however, that name is also superfluous, because he cited in synonymy two legitimate available names, *S. hypoleucum* and *S. purpureum*. The epithet "heterophyllum" is no longer available in *Stigmaphyllon*, because it has already been used for another species [*S. heterophyllum* Hooker = *S. littorale* Adr. Juss.]. Matters were also confused by Lamarck (1783), who misapplied a Linnaean name, *B. fulgens*, to the species here discussed [*B. fulgens* L. = *S. emarginatum* (Cav.) Adr. Juss.]. This error was noted by Cavanilles (1790), who had corresponded with J. E. Smith, then the owner of the Linnaean herbarium. Cavanilles treated the species under the name "*B. fulgens* Lam." When Jussieu (1840, 1843) published *S. fulgens*, he noted that he was basing the name on *Banisteria fulgens* in the sense of Lamarck, not Linnaeus, but also listed *B. heterophylla* Willd. and *B. splendens* DC. in synonymy; *S. fulgens* Adr. Juss. is thus a superfluous name. Niedenzu (1900, 1928) followed Jussieu and cited this species under the name "*S. fulgens* (Lam.) Juss."

W. R. Anderson (1981) also discussed the nomenclatural difficulties. He noted that the names S. *fulgens* and *S. splendens* are illegitimate and that the name *S. heterophyllum* had already been used for another species. He adopted *S. hypoleucum* Miquel, the earliest legitimate name for the variant with abaxially densely sericeous leaves, but also indicated that this name would be displaced by *S. richardianum* Adr. Juss. and *S. martianum* Adr. Juss., if their types are included in this species.

De Candolle's *B. splendens* (i.e., *B. heterophylla* Willd.) was based on the variant in which the lower leaf surfaces are very densely pubescent. De Candolle also had a specimen of the form in which the leaves are only moderately sericeous below, a Perrottet collection from French Guiana; this specimen is the type of his name *Banisteria sinuata*, also published in the *Prodromus* (1824). Jussieu (1840, 1843) made the combination in *Stigmaphyllon*, but expressed some doubts that

his concept of the species and de Candolle's *B. sinuata* were the same. Unfortunately, it proved that the Perrottet specimens that Jussieu saw at P and annotated as *S. sinuatum* belong to *S. palmatum* (Cav.) Adr. Juss., and were not duplicates of de Candolle's type of *B. sinuata*, as Jussieu believed. In Jussieu's defense, it should be noted that *S. palmatum* is also greatly variable in leaf shape and that its type, erroneously, was said to be from Hispaniola; the type of *S. palmatum* has deeply palmate laminas, whereas the Perrottet specimens Jussieu saw have unlobed leaves. Niedenzu confounded the matter further by recognizing de Candolle's *B. sinuata* as a variety, first (1900) of *S. hastatum* Griseb. [a superfluous name based on *B. angulata* Vell. (=*S. auriculatum* (Cav.) Adr. Juss.), which Grisebach misapplied to *S. littorale*] and later (1928) of *S. sagittatum* [sensu Niedenzu, including *S. hastatum*; *S. sagittatum* (Cav.) Adr. Juss. = *S. palmatum*]. Jussieu's and Niedenzu's misinterpretations of *B. sinuata* led later botanists to apply the name *S. sinuatum* to specimens of either *S. littorale* or *S. palmatum*. My recent examination of the type of *B. sinuata* confirmed that it belongs to the species here discussed, and that in *Stigmaphyllon* the correct name is *S. sinuatum* (DC.) Adr. Juss.

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NOVELTIES IN STIGMAPHYLLON (MALPIGHIACEAE) FROM SOUTH AMERICA

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The large, neotropical genus *Stigmaphyllon* (Malpighiaceae) comprises yellow-flowered vines that typically have long-petiolate elliptical to cordate leaves. The flowers are distinctive in that the lateral sepals each bear a pair of large elongate glands, the androecium is usually heteromorphic, and the three styles usually bear apical appendages, the folioles, for which the genus is named. The fruit is a schizocarp of three samaras, each with a dorsal wing. During the preparation of a monograph of *Stigmaphyllon*, I have noted eight additional new species and one new variety, all from South America, which are here described.

Stigmaphyllon adenodon var. **macropterum** C. Anderson, var. nov.—TYPE: ECUADOR. Napo: Baeza-Tena Rd, ca. 5 km N of Jondachi, ca. 1000 m, *Harling & Andersson 16398* (holotype: MICH!; isotype: GB!).

A *Stigmaphyllo adenodonte* var. *adenodonte* ala dorsali 5.3–6.5 cm longa et 1.5–2 cm lata differt.

Vine. Laminas 5–14.5 cm long, 3.5–15 cm wide, cordate or ovate or narrowly so to triangular (especially the smaller laminas), apex mucronate or acuminate-mucronate, base cordate or in smaller leaves truncate, glabrate to glabrous above, with T-shaped hairs below, margin with stipitate (nail-like) glands 0.2–0.6 mm long and apically disklike to 0.5 mm in diameter, with a pair of shallowly cupulate sessile glands at the apex of the petiole (to 3 mm below the lamina), each gland 1–2.5 mm in diameter; petioles 1.6–11.5 cm long. Flowers 15–30 (–40) per umbel or pseudoraceme, these borne in dichasia or compound dichasia or small thyrses; peduncles (0.8–) 1–2.75 times as long as pedicels. All petals with the limbs orbicular or sometimes broadly ovate, glabrous, margin erose or erose-denticulate; anterior-lateral petals: claw 2–2.5 (–3) mm long, limb 9.5–11 (–13) mm long and wide; posterior-lateral petals: claw 1.5–2.5 mm long, limb ca. 8–9 mm long and wide; posterior petal: claw (2.2–) 2.5–3 (–3.5) mm long, limb 8–8.5 (–10) mm long and wide. Stamens unequal, those opposite the posterior-petals the largest, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced or those opposite the posterior-lateral sepals with the locules equalling the connective or only slightly reduced; anthers pubescent. Anterior style 2.8–3.7 mm long, shorter than the posterior two; apex 1.8–2.4 mm long, each foliole 1.2–1.5 mm long, (0.5–) 0.8–1.1 (–1.3) mm wide, sometimes sublinear but more commonly narrowly oblong to oblong to parabolic; posterior styles 3.5–4.7 mm long, lyrate; folioles (1.3–) 1.8–2.5 mm long, (1.3–) 1.5–2.1 mm wide, oblong to subsquare. Dorsal wing of samara 5.3–6.5 cm long, 1.5–2 cm wide; nut with narrow winglets, up to 11 mm long and 3.5 mm wide, or with shallow ridges or crests, these often interconnected, nut 17–21 mm high, 12–19 mm in diameter, inflated,

locule surrounded by air chambers, areole 5.5–7 mm long, 5.5–6.5 mm wide, concave, carpophore up to 3.5 mm long. Embryo 8–10 mm long, 4.1–5 mm wide, ca. 2 times as long as wide, ovoid, outer cotyledon 12.5–15.5 mm long, 4.1–5 mm wide, the distal 2/5 folded over the inner cotyledon, inner cotyledon 3.5–7.3 mm long, 2.5–3.5 mm wide, straight.

Phenology. Collected in flower and fruit from December through February.

Distribution. Amazonian Ecuador and adjacent Peru; in wet areas, along rivers, and in rain forest and flooded forest; sea level to 1160 m.

Representative Specimens. **Ecuador.** Napo: San Pablo Aguarico, Río Shushufindi, *Lescure 2165* (MICH, NY).—Pastaza: Mera, *Harling 3779* (S). **Peru.** Amazonas: Río Cenepa above mouth of Río Huampami and prior to Chávez Valdivia, *Berlin 834* (GH, MO).

Stigmaphyllon adenodon Adr. Juss. is named for the distinctive stalked and apically flared (nail-shaped) marginal glands of the leaves. It is also characterized by its pubescent anthers, and samaras in which the enlarged nut consists of a locule surrounded by air chambers. Variety *macropterum* differs from var. *adenodon* in that the samara's wing is not reduced to a triangular winglet encircling the nut but is roughly narrowly rectangular, like that of most species.

The Peruvian collection (*Berlin 834*) here assigned to var. *macropterum* may represent, perhaps partly, a hybrid or possibly an apomictic population. It consists of fruiting branches as well as separate inflorescence branches in bud; most likely these were collected from different individuals. The samaras examined contain normal-appearing embryos and the anterior styles still retained have normal-appearing folioles. In the buds examined, the pollen is composed nearly 100% of non-staining, thick-walled, shrunken, misshapen grains. The anterior styles do not bear large folioles; the apex is only laterally expanded into a lip up to ca. 0.7 mm long and 0.5 mm wide.

Stigmaphyllon arenicola C. Anderson, sp. nov.—Type: Brazil. São Paulo: Mpio. Iguape, ca. 1 km WSW of city of Iguape, 24°43'S, 47°34'W, *Eiten & Clayton 6202* (holotype: UB!; isotypes: K! NY! SP! US!). Fig. 1.

Stigmaphyllon martianum var. β *variabile* Nied., Pflanzenreich IV. 141: 491. 1928.—Type: Brazil. São Paulo: Praia Grande near Santos, *Mosén 3350* (holotype: S!; isotypes: C! P!). The duplicates at C and P are also labeled *Glaziou 13604*; the fragments at NY (ex B) labeled *Glaziou 13604* are *S. urenifolium*.

Liana. Laminae 5.8–14.5 cm longae, 2.7–9.5 cm latae, lanceolatae vel triangulares vel ovatae vel ellipticae vel interdum 2–3-lobatae, supra glabrae vel glabratae, subtus glabrae vel glabratae vel interdum sparsim sericeae, margine eglanduloso vel sparsim glanduloso. Inflorescentia solitaria vel dichasialis constata ex umbellis, floribus in quaque umbella ca. 10–30. Pedunculi 3.5–13.5 mm longi; pedicelli 4–10.5 mm longi. Petala limbo orbiculari, margine fimbriato vel denticulato-fimbriato. Stamina heteromorpha, antheris glabris; antherae sepalis lateralibus oppositae steriles vel 1–2 loculis reductis instructae. Stylus anticus 3–4 mm longus, glaber, utroque foliolo 1.2–1.6 mm longo, 1.1–1.8 mm lato, subquadrato vel suborbiculari; styli postici 3.6–4.5 mm longi, glabri, lyrati, foliolo 2–3 mm longo, (1.7–) 2–2.6 mm lato, subquadrato vel interdum subrectangulari. Samara ala dorsali 2.8–3 cm longa, 0.9–1 cm lata; alulae laterales absentes; nux 6.5–7.5 mm alta, ca. 4.5 mm diametro.

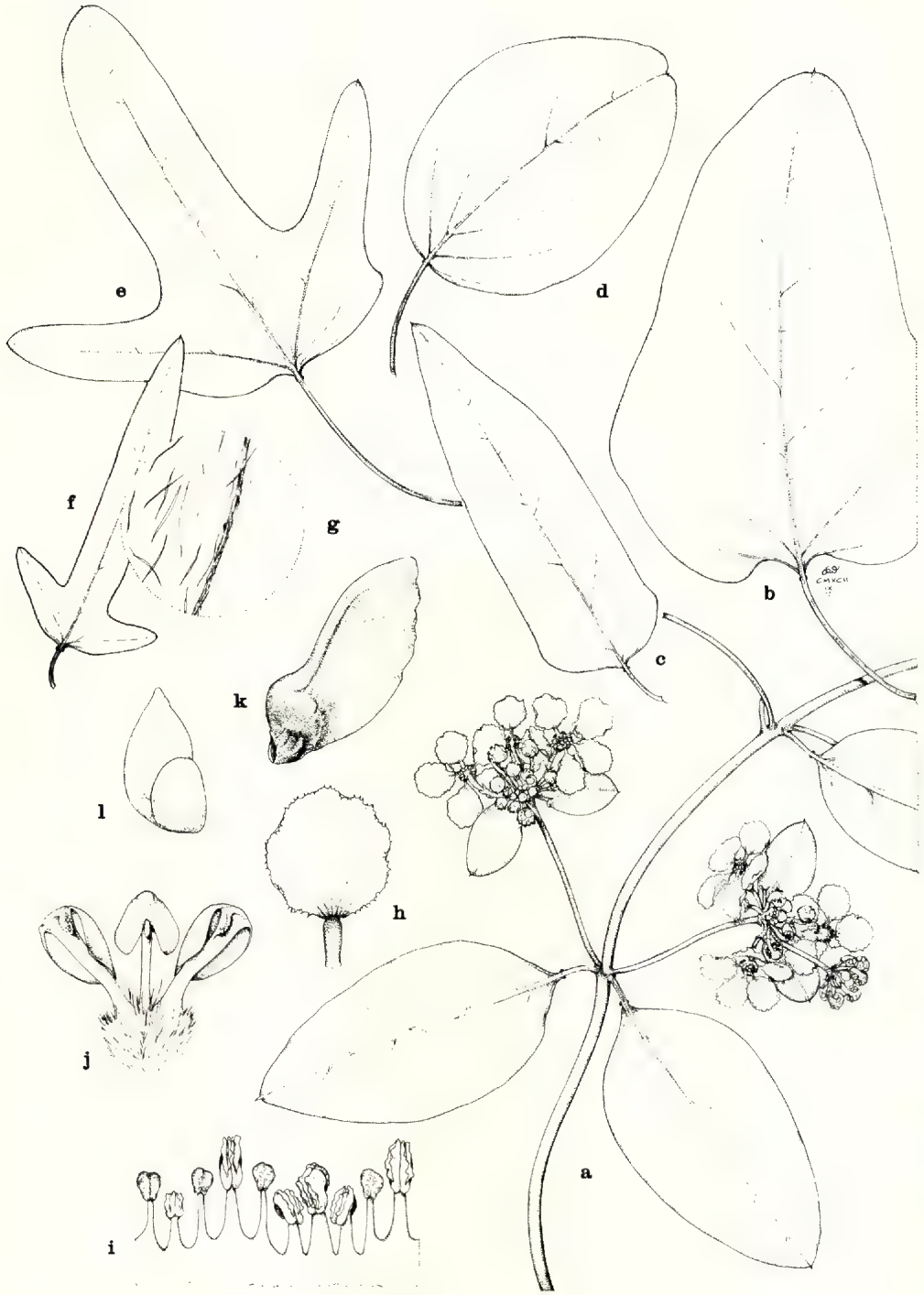

FIG. 1. *Stigmaphyllon arenicola.* a. Flowering branch (×0.5). b–f. Leaves illustrating variation of laminar shape (×0.5). g. Detail of abaxial leaf surface (×10). h. Posterior petal (×2). i. Androecium (×5); second stamen from left opposing posterior petal. j. Gynoecium (×5); posterior styles bent slightly outward to show anterior style (in center). k. Samara (×1). l. Embryo (×2.5). (Based on: a, *Eiten & Clayton 6202;* b, *Markgraf 3783;* c, f, g, *Eiten & Eiten 2800;* d, k, l, *Almeida de Jesus 1564;* e, *Anderson 11197;* h, i, *Angeli 475;* j, *Smith & McWilliams 15354.*)

Vine to 4 m. Laminas 5.8–14.5 cm long, 2.7–9.5 cm wide, lanceolate to triangular to ovate to elliptical but often 2–3-lobed, apex acute-mucronate to obtuse-mucronate or emarginate-mucronate, base attenuate or truncate to cordate, glabrous or glabrate above, glabrous or glabrate or sometimes sparsely to rarely moderately sericeous below but with abundant hairs along the margin (the hairs sometimes sloughed off in older laminas), margin eglandular or sometimes with irregularly spaced sessile glands (0.2–0.3 mm in diameter) borne adjacent to the margin below, the lateral lobes sometimes terminating in a filiform gland up to 0.1 mm long, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.1–2.5 mm in diameter; petioles 1–11 cm long; stipules 0.5–1.7 mm long. Flowers ca. 10–30 per umbel, these borne solitary or in dichasia or compound dichasia; peduncles 3.5–13.5 mm long; pedicels 4–10.5 mm long; peduncles 0.6–1.6 times as long as the pedicels; bracts 1–2 mm long, 0.5–1.4 mm wide, triangular or narrowly so; bracteoles 1–1.8 mm long, 0.8–1.1 mm wide, triangular. Sepals 2.1–2.5 mm long, 2–2.7 mm wide, glands 1.7–2.7 (–3.2) mm long, 1–1.5 mm wide. All petals with the limbs orbicular, glabrous, margin fimbriate or denticulate-fimbriate, teeth/fimbriae up to 0.3 (–0.5) mm long; anterior-lateral petals: claw 2–3 mm long, limb 12–14 mm long and wide; posterior-lateral petals: claw 1–1.8 mm long, limb 10–12.5 mm long and wide; posterior petal: claw 2.5–3.7 mm long, apex usually indented, limb 9–10 mm long and wide, sometimes margin near the base with 1–2 stout gland-tipped fimbriae per side, these ca. 0.5 mm long, ca. 0.2 mm wide. Stamens unequal, those opposite the posterior-lateral petals the largest, those opposite the lateral sepals eloculate or sometimes the enlarged connective with 1 or rarely 2 reduced locules; anthers glabrous. Anterior style 3–4 mm long, shorter than the posterior two or sometimes subequal, glabrous; apex 1.3–1.9 mm long, each foliole 1.2–1.6 mm long, 1.1–1.8 mm wide, subsquare or suborbicular. Posterior styles 3.6–4.5 mm long, glabrous or with scattered hairs in the proximal 1/3–1/2, lyrate; foliole 2–3 mm long, (1.7–) 2–2.6 mm wide, subsquare to sometimes subrectangular. Dorsal wing of samara 2.8–3 cm long, 0.9–1 cm wide, upper margin with a blunt tooth; nut 6.5–7.5 mm high, ca. 4.5 mm in diameter, smooth or with a few spurs, areole 2.7–4.5 mm long, 3–3.5 mm wide, concave, carpophore up to 3.5 mm long. Embryo 6.5–8.1 mm long, 1.5–2 times as long as wide, ovoid, outer cotyledon 8–9.5 mm long, 4.1–4.3 mm wide, the distal 2/3 folded over the inner cotyledon, inner cotyledon 4–5 mm long, 2.9–3.5 mm wide, straight.

Phenology. Collected in flower throughout the year, in fruit from May through July.

Distribution. Southeastern Brazil, Rio de Janeiro to Paraná; along beaches, on dunes, in restingas, one report from vicinity of coastal swamp forest; sea level to 340 m.

Representative Specimens. **Brazil.** Paraná: Mpio. Guaraqueçaba, Tagaçaba, *Hatschbach 42721* (MICH); Ilha do Mel, Prainha, *Kummrow 1334* (MBM); Ilha do Mel, Mpio. Panaguá, *Ribas 9* (MICH).—Rio de Janeiro: Lagoa de Marapendi, estrada do Autódromo, *Almeida de Jesus 1564* (RB); restinga ca. 11 km W of Barra da Tijuca, *Anderson 11197* (MBM, MICH); restinga de Jacarepaguá, *Angeli 475* (MICH); restinga de Jacarepaguá, Pedro de Itauna, *Araujo 657 & Peixoto 490* (MICH, RB); Recreio do Bandeirantes, *Lutz R23973* (R); restinga de Sernambetiba, *Markgraf 3783* (RB); Recreio dos Bandeirantes, Jacarepaguá, *Palacios et al. 4061* (R); 1–3 km S of Lidice, *Smith & McWilliams 15354* (MICH, R); pr. Bonfim, *Trinta 882 & Fromm 1958* (R).—São Paulo: Iguape, Morro das Pedras, *Brade 7898* (R); Santos, *Curran 13* (US); between Ubatuba and Caraguatuba, 10 m, *Davis et al. D59894* (E, MBM); Mpio. Mongaguá, at Mongaguá, *Eiten & Eiten 2542* (SP);

Mpio. Caraguatatuba, SW of Caraguatatuba, *Eiten & Eiten 2800* (SP); Mongaguá, praia de Suarão, *Kirizawa 67* (SP); Mpio. Ilha do Cardoso, *Leitão Filho 10792* (SP); Praia Grande, Praia Piassabusú, *Löfgren 4160* (SP); Ubatuba, *C. Smith 4844* (SP); rd between São Vicente and Itaipu, 24°00'S, 46°24'W, *L. B. Smith 2000* (GH); Ilha Bela, Serra do Castelhanos, *Sucre 6982* (MICH, SP).

Stigmaphyllon arenicola, a species of sandy areas of coastal southeastern Brazil, is notable for its polymorphic leaves. The laminas vary from lanceolate to triangular to ovate to elliptical but may also be 2–3-lobed. They are most commonly very sparsely sericeous to glabrate below but sometimes are glabrous or sericeous. Mostly, the mature laminas are glabrous to glabrate, whereas the younger laminas and the reduced ones near and in the inflorescences are at least sparsely sericeous; however, plants with all of the laminas abaxially sericeous or glabrous also occur. The anthers are glabrous. Those of stamens opposite the lateral sepals usually lack locules, but sometimes the enlarged connectives bear 1 or rarely 2 reduced locules. *Stigmaphyllon arenicola* might be confused with the partly sympatric *S. lalandianum*, in which the laminas are sericeous abaxially. *Stigmaphyllon lalandianum* is readily separated by its small flowers with erose petals (the lateral limbs up to only 10 mm in diameter); all stamens bear locules, and the styles are efoliolate or bear only tiny folioles less than 1 mm long.

Stigmaphyllon crenatum C. Anderson, sp. nov.—TYPE: BRAZIL. Espírito Santo: Rio Pancas, Aldeiamento dos Indios, *Buena 156* (holotype: R-37607!). Fig. 2.

Liana. Laminae 5.5–13.5 cm longae, 4.5–11.3 cm latae, late ellipticae vel suborbiculares, margine crenato, sinubus glanduloso, laminae juniores et inflorescentiae supra dense sericeae et subtus pilis T-formibus dense instructae, laminae vetustiores utrinque glabrae vel glabratae. Inflorescentia solitaria vel dichasialis vel thrysiformis constata ex umbellis, floribus in quaque umbella ca. 10. Petala limbo orbiculari, margine eroso-denticulato. Stamina heteromorpha, antheris glabris. Stylus anticus ca. 2 mm longus, apice ca. 2 mm longo, ca. 0.4 mm lato, lineari; styli postici ca. 3.2 mm longi, lyrati, foliolo ca. 1.2 mm longo latoque, parabolico. Samara ignota.

Vine. Laminas 5.5–13.5 cm long, 4.5–11.3 cm wide, broadly elliptical to suborbicular, apex obtuse or emarginate or emarginate-mucronate or mucronate, base truncate to cordate, densely sericeous above and densely beset with T-shaped hairs below in young leaves and those near the inflorescence, the older laminas glabrate to glabrous above and below, margin irregularly crenate, each sinus with a circular flush gland 0.7–1.7 mm in diameter, with a pair of glands borne halfway on the petiole, these flush with the epidermis and margined, each gland 1.3–2.5 mm in diameter; petioles up to 2 mm long; stipules absent (?). Flowers ca. 10 per umbel, these borne solitary or in dichasia or compound dichasia or small thyrses; peduncles 5–7 mm long (?); pedicels ca. 6 mm long (?); peduncles subequal to the pedicels (?); bracts 0.8–1.2 mm long and wide, broadly triangular; bracteoles 1–1.3 mm long, 0.8–1 mm wide. Sepals ca. 3 mm long, ca. 2 mm wide, glands 2–2.3 mm long, ca. 1 mm wide. Lateral petals with the limbs orbicular, glabrous, margin erose-denticulate; anterior-lateral petals: claw ca. 3 mm long, limb 13–14 mm long and wide; posterior-lateral petals: claw ca. 1.5 mm long, limb ca. 12 mm long and wide; posterior petal not seen. Stamens unequal, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous (anthers of posterior-lateral and posterior stamens only seen in

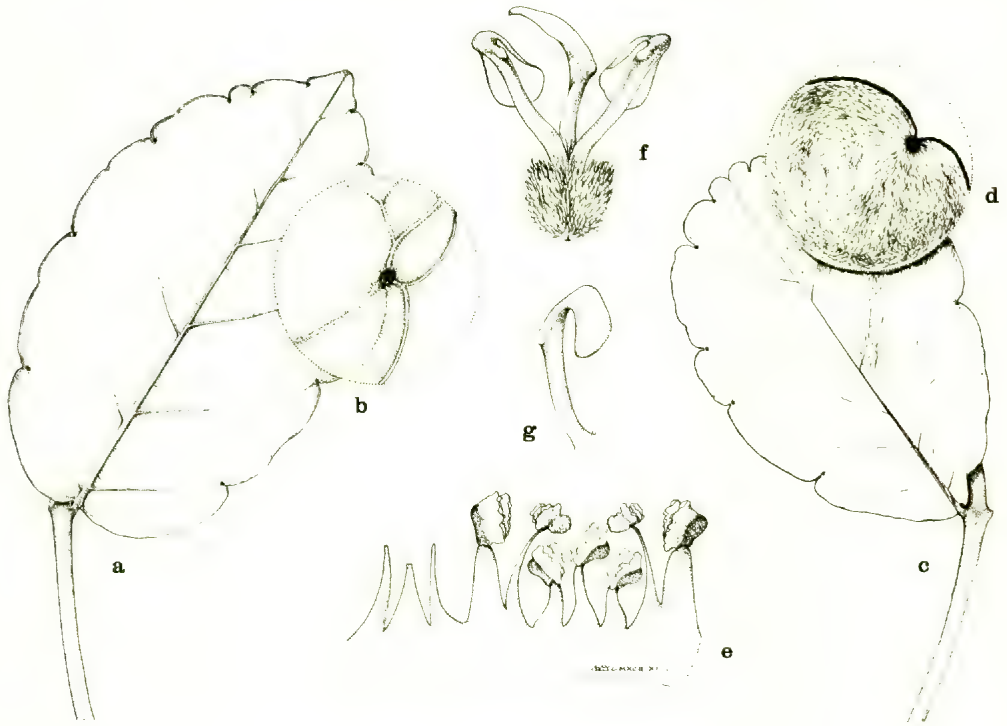

FIG. 2. *Stigmaphyllon crenatum*. a. Glabrous leaf (×0.5). b. Detail of abaxial surface of glabrous leaf with marginal gland (×2). c. Pubescent leaf (×0.5). d. Detail of abaxial surface of pubescent leaf with marginal gland (×2). e. Androecium (×5); fourth stamen from right opposing anterior sepal; anthers of stamens opposing posterior petal and posterior-lateral sepals not seen. f. Gynoecium (×7.5); anterior style in center. g. Lateral view of posterior style (×7.5). (Based on: a, b, *Duarte 400;* c–g, *Buena 156.*)

young bud). Anterior style ca. 2 mm long, shorter than the posterior two, terete proximally, laterally flattened in the distal 1/4, glabrous; apex ca. 2 mm long including a spur ca. 1 mm long, ca. 0.4 mm wide, linear, folioles absent. Posterior styles ca. 3.2 mm long, terete, with scattered hairs in the proximal 1/4, lyrate; foliole ca. 1.2 mm long and wide, parabolic to triangular. Samara not seen.

Phenology. Collected in flower in July, November, and December.

Distribution. Northern Espírito Santo, Brazil; in campo rupestre, on rock faces.

Additional Specimens Examined. **Brazil.** Espírito Santo: Mpio. Venecia, *Duarte 4000* (RB); Colatina, Rio Pancas, *J. Kuhlmann 6651* (RB).

Stigmaphyllon crenatum is the only species in the genus with nearly sessile deeply crenate leaves. Each sinus is marked by a gland up to 1.7 mm in diameter. In many species, leaves of older plants have shed some or sometimes all of the vesture. This phenomenon is apparently particularly strongly expressed in *S. crenatum*. The type, collected in July, consists of three flowering branchlets, one of which bears two pairs of leaves. These laminas are densely sericeous above; the abaxial dense silvery pubescence is composed of T-shaped hairs. In *Duarte 4000* and *J. Kuhlmann 6651*, collected in November and December, only the dichasially branched inflorescence axes are retained, and the leaves are glabrous, though on some laminas patches of hairs remain; the immature leaves at branch apices bear

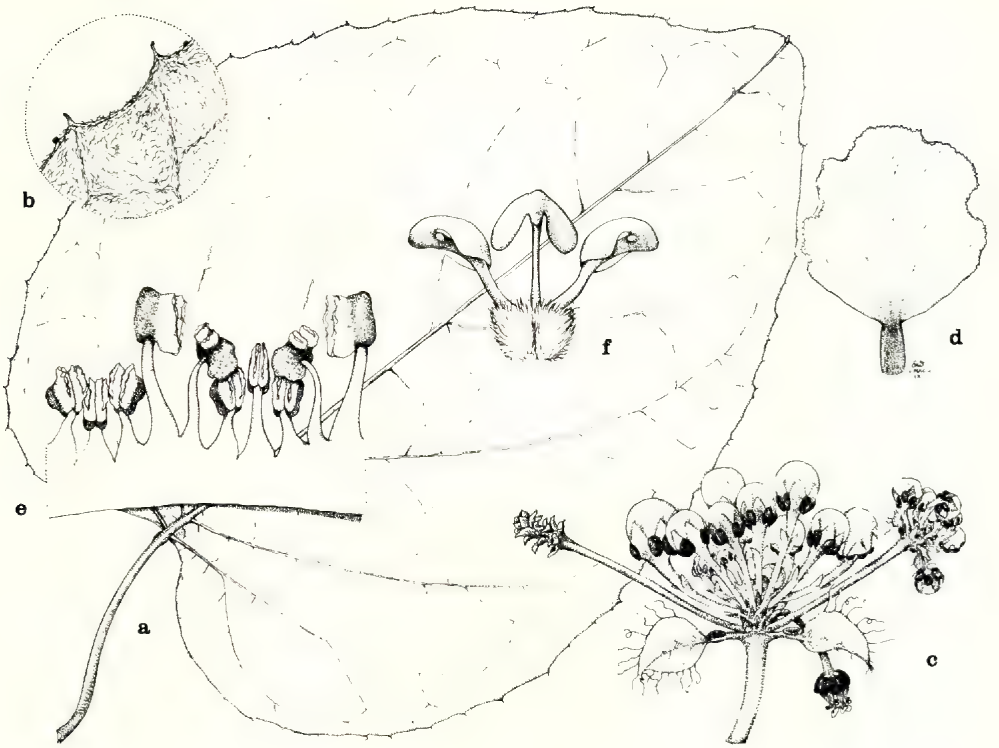

FIG. 3. *Stigmaphyllon ecuadorense*. a. Large leaf (×0.5). b. Detail of abaxial leaf surface (×2.5). c. Portion of inflorescence (×1). d. Posterior petal (×2). e. Androecium (×5); second stamen from left opposing posterior petal. f. Gynoecium (×5); posterior styles bent slightly outward to show anterior style (in center). (Based on: a, b, *Steiner 219;* c–f, *Wunderlin et al. 8736.*)

the typical vesture. The flowers are distinctive in that the apex of the anterior style is drawn out into a long claw but lacks folioles; the posterior styles are both foliolate. The only mature flower on the type lacks the posterior petal and the anthers of the posterior and posterior-lateral stamens. Examination of a bud indicates that these anthers all have two locules, but it was not apparent whether the anthers of the posterior-lateral stamens would bear an enlarged connective at maturity.

Stigmaphyllon ecuadorense C. Anderson, sp. nov.—TYPE: ECUADOR. Manabi: 44 km W of El Empalme on rd from Quevedo to Portoviejo, 1100 ft, 6 Aug 1980, *Wunderlin et al. 8736* (holotype: SEL!; isotype: MO!). Fig. 3.

Liana. Laminae 10–23 cm longae, 8.5–20.5 cm latae, late ovatae vel late cordatae vel suborbiculares, supra glabrae vel glabratae, subtus tomentosae, margine sparsim glanduloso. Inflorescentia dichasialis constata ex pseudoracemis, floribus in quoque pseudoracemo ca. 20–40. Pedunculi 7.5–13.5 mm longi; pedicelli 8–10 mm longi. Petala limbo orbiculari, margine eroso vel eroso-denticulato. Stamina heteromorpha, antheris glabris; antherae sepalis antico-lateralibus oppositae loculis reductis instructae. Stylus anticus ca. 3.5 mm longus, glaber, utroque foliolo 1.6–2 mm longo, ca. 1.6–1.7 mm lato, subquadrato vel subrectangulari; styli postici 4.3–4.7 mm longi, glabri, lyrati, foliolo ca. 2.5 mm longo, 2.3–2.5 lato, suborbiculari. Samara immatura ala dorsali ca. 4 cm longa, ca. 1.5 cm lata; alulae laterales ca. 8 mm longae, ca. 3.5 mm latae.

Vine. Laminas 10–23 cm long, 8.5–20.5 cm wide, broadly ovate to broadly cordate to suborbicular, apex emarginate-mucronate, base truncate in the smaller laminas to cordate in the larger, glabrate to glabrous above, tomentose below, margin very shallowly dentate and the teeth terminating in filiform glands (up to 4 mm long, broken in large leaves) or irregularly spaced subsessile to stalked glands (0.2–0.4 mm in diameter, 0.1–0.5 mm long), with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.7–2.6 mm in diameter; petioles 3–7.5 cm long; stipules 0.6–0.8 mm long. Flowers ca. 20–40 per pseudoraceme, these borne in compound dichasia; peduncles 7.5–13.5 mm long; pedicels 8–10 mm long; peduncles 0.9–1.6 times as long as the pedicels; bracts 1.4–2.2 mm long, 1–1.5 mm wide, triangular; bracteoles 1.5–2.2 mm long, 1.1–1.6 mm wide, oblong. Sepals 2.5–3 mm long and wide, glands 3–3.5 mm long, ca. 1.5 mm wide. All petals with the limbs orbicular, glabrous, margin erose or erose-denticulate, the teeth up to 0.3 mm long; anterior-lateral petals: claw ca. 3 mm long, limb 14–15 mm long and wide; posterior-lateral petals: claw 1.6–2 mm long, limb ca. 13 mm long and wide; posterior petal: claw ca. 3 mm long, apex indented, limb ca. 12 mm long and wide. Stamens unequal, those opposite the posterior-lateral petals the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style ca. 3.5 mm long, shorter than the posterior two, terete, glabrous; apex 1.9–2.2 mm long; each foliole 1.6–2 mm long, ca. 1.6–1.7 mm wide, subsquare to subrectangular. Posterior styles 4.3–4.7 mm long, glabrous, lyrate; foliole ca. 2.5 mm long, 2.3–2.5 mm wide, suborbicular. Immature samara with a dorsal wing up to 4 cm long and 1.5 cm wide, the nut with a pair of lateral winglets up to 8 mm long and 3.5 mm wide.

Phenology. Collected in flower in July and August, in young fruit in August.

Distribution. Ecuador, Manabi; brushy roadsides; 300–400 m.

Additional Specimens Examined. **Ecuador.** Manabi: 7.5 km W of Río Daule at Pichincha, *Steiner 219* (DAV, MICH).

Stigmaphyllon ecuadorense is a showy species notable for its large leaves and large flowers disposed in pseudoracemes. The laminas are tomentose below and have a shallowly dentate margin, the teeth terminating in filiform glands. The limbs of the lateral petals are 13–15 mm in diameter and have an erose or erose-denticulate margin; the anthers of stamens opposite the posterior-lateral sepals have the connective and locules about equally long. The only other species of *Stigmaphyllon* reported from Manabi are *S. eggersii* C. Anderson and *S. ellipticum* (H. B. K.) Adr. Juss., which also have large flowers but with fimbriate to lacerate limbs; the anthers of stamens opposite the lateral sepals have the connective enlarged and the locules reduced. Their laminas are borne on short petioles (up to 3 cm long) and have eglandular margins. *Stigmaphyllon ecuadorense* might be confused with *S. sinuatum* (DC.) Adr. Juss., of the Amazonian region, in which the flowers are also borne in pronounced pseudoracemes and the anthers of stamens opposite the posterior-lateral sepals are unmodified. *Stigmaphyllon sinuatum* is readily separated by the sericeous abaxial pubescence of the laminas.

Stigmaphyllon eggersii C. Anderson, sp. nov.—Type: Ecuador. Manabi: Estero Perro Muerto, Machalilla National Park, below San Sebastián, 01°36'N, 80°42'W, *Gentry & Josse 72667* (holotype: M!; isotypes: A! US!).

Liana. Laminae 5.3–18 cm longae, 3–10.7 cm latae, ovatae vel late ellipticae, supra glabrae vel interdum sparsim sericeae, subtus pilos T-formes ferentes, margine eglanduloso. Inflorescentia solitaria vel dichasialis constata ex pseudoracemis, floribus in quoque pseudoracemo ca. 8–15. Pedunculi 1.8–9 mm longi; pedicelli 6–9 mm longi. Petala limbo orbiculari, margine fimbriato vel fimbriato-lacerato. Stamina heteromorpha, antheris glabris; antherae sepalis lateralibus oppositae loculis reductis instructae. Stylus anticus 3–3.3 mm longus, glaber, utroque foliolo 0.3–0.7 mm longo, 0.4–0.5 mm lato, parabolico; styli postici ca. 3.2 mm longi, glabri, foliolo 0.5–1 mm longo, 0.4–0.8 mm lato, parabolico. Samara immatura ala dorsali ca. 2.3 cm longa, ca. 1.2 cm lata; alulae laterales absentes.

Vine. Laminas 5.3–18 cm long, 3–10.7 cm wide, ovate to broadly elliptical, apex mucronate or emarginate-mucronate to acuminate, base cordate to truncate, glabrous above, with T-shaped hairs below, margin eglandular, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1–1.7 mm in diameter; petioles 1.2–3 cm long; stipules 0.5–1.2 mm long. Flowers ca. 8–15 per condensed pseudoraceme, these borne solitary or in dichasia or compound dichasia; peduncles 1.8–9 mm long, sericeous or sparsely so; pedicels 6–9 mm long, glabrous; peduncles 0.3–1.3 times as long as the pedicels; bracts 1.2–1.8 mm long, 0.7–1.1 mm wide, triangular; bracteoles 1–1.6 mm long, 0.7–1 mm wide, ovate. Sepals 2.5–3 mm long, 2.5–2.8 mm wide, glands 1.8–2.5 mm long, 0.8–1.3 mm wide. All petals with the limbs orbicular, glabrous, margin fimbriate to fimbriate-lacerate, fimbriae and teeth up to 1.6 mm long; anterior-lateral petals: claw 2.5–2.8 mm long, limb 14–15 mm long and wide; posterior-lateral petals: claw ca. 2 mm long, limb 13–14 mm long and wide; posterior petal: claw 3.6–4.5 mm long, apex indented, limb 10–12 mm long and wide. Stamens unequal, those opposite the anterior-lateral sepals with the longest filaments, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3–3.3 mm long, subequal to the posterior two, glabrous; apex 1.1–1.5 mm long, folioles variable in size, each foliole 0.3–0.7 mm long, 0.4–0.5 mm wide, parabolic. Posterior styles ca. 3.2 mm long, glabrous, slightly lyrate; foliole 0.5–1 mm long, 0.4–0.8 mm wide, parabolic. Mature samara not seen; dorsal wing of nearly mature samara ca. 2.3 cm long, ca. 1.2 cm wide, upper margin with a shallow blunt tooth, lateral winglets absent; nut ca. 4.5 mm high, ca. 3.5 mm in diameter, areole ca. 3.5 mm long, ca. 2.3 mm wide, concave but convex at center, carpophore up to ca. 1 mm long. Embryo not seen.

Phenology. Collected in flower in January and October, in immature fruit in January.

Distribution. Lowlands of Ecuador (Guayas, Manabi); in wet forest and matorral; sea level to 470 m.

Additional Specimens Examined. **Ecuador**. Guayas: Balao, Jan 1892, *Eggers 14335* (A, M, US); Cantón Naranjal, camino de Santa Rosa de Flandres a Puerto Baquerizo, *Valverde 880* (MO).—Manabi: Rd Santa Elena-Jipijapa, Río Pital at Puerto López, 01°34'S, 80°48'W, *Holm-Nielsen et al. 27837* (AAU).

Stigmaphyllon eggersii is most similar to the widespread and sympatric *S. ellipticum*, with which it shares large flowers with fimbriate-lacerate petals. They are most readily separated by their leaf pubescence. The laminas of *S. eggersii* are pubescent with T-shaped hairs below, whereas those of *S. ellipticum* are sparsely sericeous below and usually appear glabrous to the naked eye.

This species is named for the Danish botanist Heinrich Franz Alexander von Eggers (1844–1903), who first collected it.

Stigmaphyllon glabrum C. Anderson, sp. nov.—TYPE: BRAZIL. Espírito Santo: Mpio. Castelo, estrada do Bocó, 20 Aug 1987, *Hatschbach 51343* (holotype: MBM!; isotype: MICH!).

Liana. Laminae 14.2–15.3 cm longae, ca. 12 cm latae, utrinque glabrae, margine sparsim glanduloso, laminae caulinae 5–7-pinnatifidae, laminae parvae inflorescentiae non lobatae, ovatae vel ellipticae. Inflorescentia dichasialis constata ex umbellis, floribus in quaque umbella ca. 15–20. Pedunculi 5–6 mm longi; pedicelli 7–9.5 mm longi. Petala limbo orbiculari, margine fimbriato. Stamina subaequalia, antheris glabris. Stylus anticus ca. 3.2 mm longus, apice ca. 1 mm longo, ca. 0.2 mm lato, lineari; styli postici ca. 3.5 mm longi, lyrati, apice ca. 0.7 mm longo, ca. 0.1 mm lato, lineari. Samara immatura ala dorsali longa, alulae laterales absentes.

Vine. Laminas 14.2–15.3 cm long, ca. 12 cm at widest part, pinnately 5–7-lobed, the smaller leaves associated with the inflorescence unlobed and elliptical to ovate, apex of each lobe terminating in a filiform gland, base auriculate, glabrous above and below, margin with filiform glands and rarely also with a few irregularly spaced sessile glands ca. 0.4 mm in diameter, with a pair of prominent stalked glands at the apex of the petiole, each gland 0.5–0.7 mm long, 1.5–2.2 mm in diameter; petioles ca. 6 cm long; stipules not seen. Flowers ca. 15–20 per umbel, these borne in compound dichasia; peduncles 5–6 mm long; pedicels 7–9.5 mm long; peduncles 0.6–0.8 times as long as the pedicels; bracts 1.3–1.7 mm long, 0.9–1 mm wide, triangular; bracteoles 1.5–1.8 mm long, 1–1.3 mm wide, triangular. Sepals ca. 3 mm long, ca. 2.8 mm wide, glands ca. 1.5 mm long, ca. 1 mm wide. All petals with the limbs orbicular, glabrous, suffused with red (?), margin fimbriate, fimbriae up to 1 mm long; anterior-lateral petals: claw ca. 2.5 mm long, limb 15–16 mm long and wide; posterior-lateral petals: claw ca. 1.5 mm long, limb 14–15 mm long and wide; posterior petal: claw ca. 4 mm long, apex indented, limb ca. 10 mm long and wide. Stamens unequal in size but subequal in shape, those opposite the anterior-lateral sepals the largest; anthers glabrous. Anterior style ca. 3.2 mm long, slightly shorter than the posterior two, glabrous; apex ca. 1 mm long including a spur ca. 0.1 mm long, linear, folioles absent. Posterior styles ca. 3.5 mm long, glabrous or with a few scattered hairs in the proximal 1/2, lyrate; apex ca. 0.7 mm long, blunt distally, folioles absent. Immature samara with a large flared dorsal wing, nut without lateral winglets or ornamentation.

Stigmaphyllon glabrum is known only from the type. It is distinguished by its pinnately lobed and glabrous leaves, long-fimbriate petals, and efoliolate styles. The androecium is unusual in that the stamens opposite the anterior-lateral sepals have longer filaments than the ones opposite the posterior-lateral petals; in most species, the reverse is true. *Stigmaphyllon urenifolium* Adr. Juss. of Minas Gerais and central Bahia is very similar, but the laminas are abundantly pubescent with T-shaped hairs below instead of glabrous.

Stigmaphyllon goudotii C. Anderson, sp. nov.—TYPE: COLOMBIA. Antioquia: vicinity of Medellín, Los Micos, 18 Dec 1927, *Toro 809* (holotype: NY!). Fig. 4.

Liana. Laminae 8.2–13 cm longae, 5.5–10.5 cm latae, ovatae vel cordatae, supra glabrae, subtus pilos T-formes sparsos ferentes, margine sparsim glanduloso.

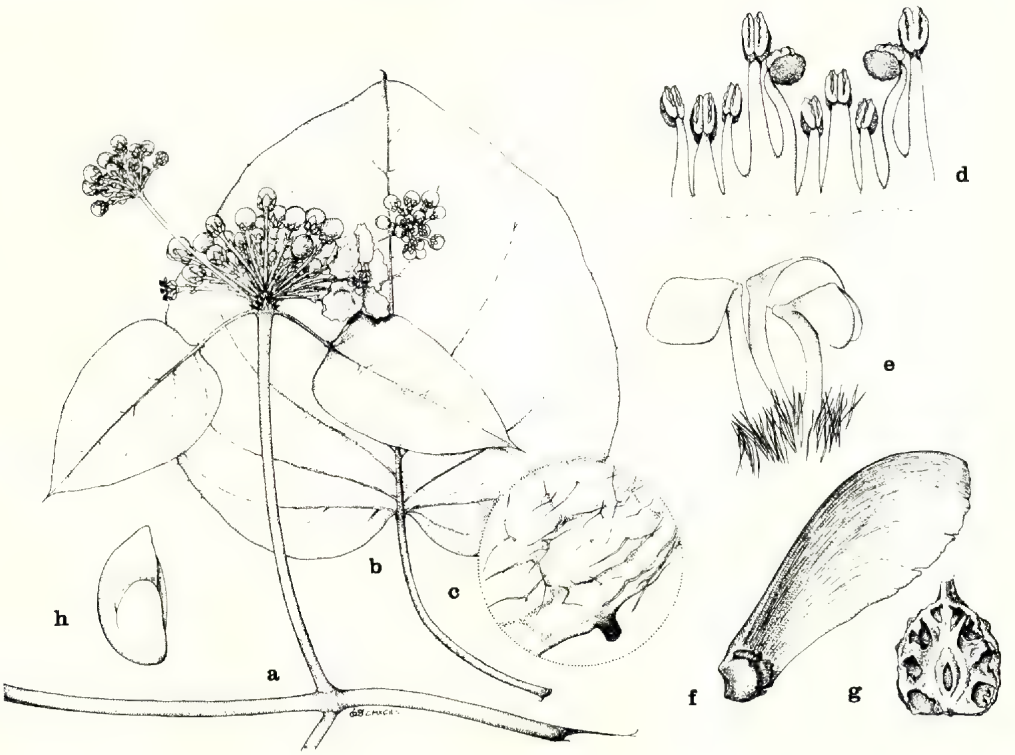

FIG. 4. *Stigmaphyllon goudotii.* a. Flowering branch (×0.5). b. Large leaf (×0.5). c. Detail of abaxial leaf surface (×10). d. Androecium (×5); second stamen from left opposing posterior petal. e. Gynoecium (×5); anterior style at right. f. Samara (×0.75). g. Longitudinal section through nut to show locule surrounded by air chambers (×1.5). h. Embryo (×2.5). (Based on: a, d, e, *Toro 809;* b, c, f, g, *Goudot s.n.;* h, *Holton 795.*)

Inflorescentia dichasialis vel thyrsiformis constata ex pseudoracemis, floribus in quoque pseudoracemo ca. 35–50. Pedunculi 15–21 mm longi; pedicelli 4–5.5 mm longi. Petala limbo orbiculari, margine eroso. Stamina heteromorpha, antheris glabris; antherae sepalis antico-lateralibus oppositae 1–2 loculis reductis instructae. Stylus anticus ca. 3.5 mm longus, utroque foliolo ca. 1.5 mm longo, ca. 1.2 mm lato, elliptico vel parabolico; styli postici ca. 4.2 mm longi, lyrati, foliolo ca. 2 mm longo latoque, subquadrato. Samara ala dorsali 4.5–5.5 cm longa, 1.9–2.2 cm lata; alulae laterales absentes; nux usque ad 15 mm alta, usque ad ca. 10 mm diametro, latere utroque alulis vel calcaribus vel cristaris instructa.

Vine. Laminas 8.2–13 cm long, 5.5–10.5 cm wide, ovate to cordate, apex acuminate, base truncate to cordate, glabrous above, sparsely pubescent with T-shaped hairs below, margin eglandular or with irregularly spaced prominent glands (0.2 mm in diameter and long), with a pair of shallowly cupulate glands at the apex of the petiole, each gland 1–1.5 mm in diameter, up to 0.3 mm high; petioles 3.2–6.5 cm long; stipules 0.7–0.8 mm long. Flowers ca. 35–50 per pseudoraceme, these borne in dichasia or compound dichasia or small thyrses; peduncles 15–21 mm long; pedicels 4–5.5 mm long; peduncles (1.5–) 3.4–4.2 times as long as the pedicels; bracts 1.8–2.2 mm long, 0.8–1.1 mm wide, narrowly triangular; bracteoles 1.6–2 mm long, 0.8–1 mm wide, triangular. Sepals ca. 2.2 mm long and wide, glands ca. 2 mm long, ca. 1.2 mm wide. All lateral petals with the limbs orbicular, glabrous, margin erose; anterior-lateral petals: claw ca. 1 mm long, limb ca. 10 mm long and wide; posterior-lateral petals: claw ca. 2.3 mm long, limb ca. 12 mm

long and wide; posterior petal: claw ca. 3 mm long, apex indented, limb ca. 10 mm long, ca. 8 mm wide, obovate. Stamens unequal, those opposite the posterior-lateral petals the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style ca. 3.5 mm long, shorter than the posterior two, glabrous; apex 1.5 mm long, each foliole ca. 1.5 mm long, ca. 1.2 mm wide, elliptical to parabolic. Posterior styles ca. 4.2 mm long, glabrous, lyrate; foliole ca. 2 mm long and wide, subsquare. Dorsal wing of samara 4.5–5.5 cm long, 1.9–2.2 cm wide, upper margin with a shallow blunt tooth or without a tooth; nut bearing 1–2 rectangular lateral winglets, these 2–5 mm long, 2–3 mm wide, and/or spurs (ca. 1 mm long) and crests; nut to 15 mm high, to ca. 10 mm in diameter, locule surrounded by air chambers, areole ca. 3 mm long and wide, concave, carpophore up to 8 mm long. Embryo ca. 8 mm long, ca. 2 times as long as wide, ovoid, outer cotyledon ca. 13 mm long, ca. 4 mm wide, the distal 2/5 folded over the inner cotyledon, inner cotyledon ca. 5.5 mm long, ca. 2.5 mm wide, straight.

Phenology. Collected in flower in December, in fruit in February and November.

Distribution. Colombia (Antioquia, Tolima, and Valle); in dry tropical forest; 1350 m.

Additional Specimens Examined. **Colombia.** Antioquia: Mpio. Giraldo, Corregimiento Manglares, 8 km de Manglares, via Santa Fé-Mutatá, 06°40'N, 75°55'W, *Callejas et al. 5608* (MICH).—Tolima: Ibague, El Tejas, *Goudot s.n.* (P).—Valle: La Paila, *Holton 795* (K, NY).

Stigmaphyllon goudotii is distinguished by its large compound inflorescences composed of 35–50-flowered pseudoracemes and large samaras. Only the stamens opposite the anterior-lateral sepals have the connective enlarged and the locules somewhat reduced; all anthers are glabrous. The samara is unusual in that the thick-walled locule is surrounded by air chambers and contains a large embryo.

This species is named for the French naturalist Justin Goudot, who first collected it during his explorations of Colombia from 1825 until 1842 (Lasègue 1845).

Stigmaphyllon jobertii C. Anderson, sp. nov.—Type: Brazil. Piauí: Nazareth, Rio Piauí, 1877–78, *Jobert 1114* (holotype: P!). Fig. 5.

Liana. Laminae 6.5–10.3 cm longae, 5.5–7 cm latae, cordatae, supra glabrae, subtus glabrae vel glabratae vel sparsissime sericeae, margine eglanduloso, petiolo glandulibus binatis stipitatis instructo. Inflorescentia dichasialis constata ex pseudoracemis, floribus in quoque pseudoracemo ca. 10–15. Pedunculi 2–2.5 mm longi; pedicelli 5.6–6.5 mm longi. Petala ignota. Stamina heteromorpha, antheris glabris. Stylus anticus ca. 2.6 mm longus, utroque foliolo ca. 1.2 mm longo, ca. 0.8 mm lato, triangulari; styli postici ca. 3 mm longi, parum lyrati, foliolo ca. 1.3 mm longo, ca. 0.6 mm lato, parabolico. Samara ala dorsali ca. 2.6 cm alta, ca. 1.4 cm lata; alulae laterales absentes; nux 6.5–7.5 mm alta, 3.5–4.5 mm diametro, loculo in contextu spongioso incluso.

Vine. Laminas 6.5–10.3 cm long, 5.5–7 cm wide, cordate, apex apiculate, base cordate to auriculate in the largest laminas, glabrous above, very sparsely sericeous but soon becoming glabrate to glabrous below, margin eglandular, with a pair of stalked glands on the petiole up to 3 mm below the base of the lamina, often inserted obliquely, each gland 0.8–1.5 mm long, 0.6–0.9 mm in diameter; petioles from 3 cm long (petioles of larger leaves not seen); stipules 0.6–1 mm long. Flowers ca. 10–15 per pseudoraceme, these borne in dichasia or small thyrses;

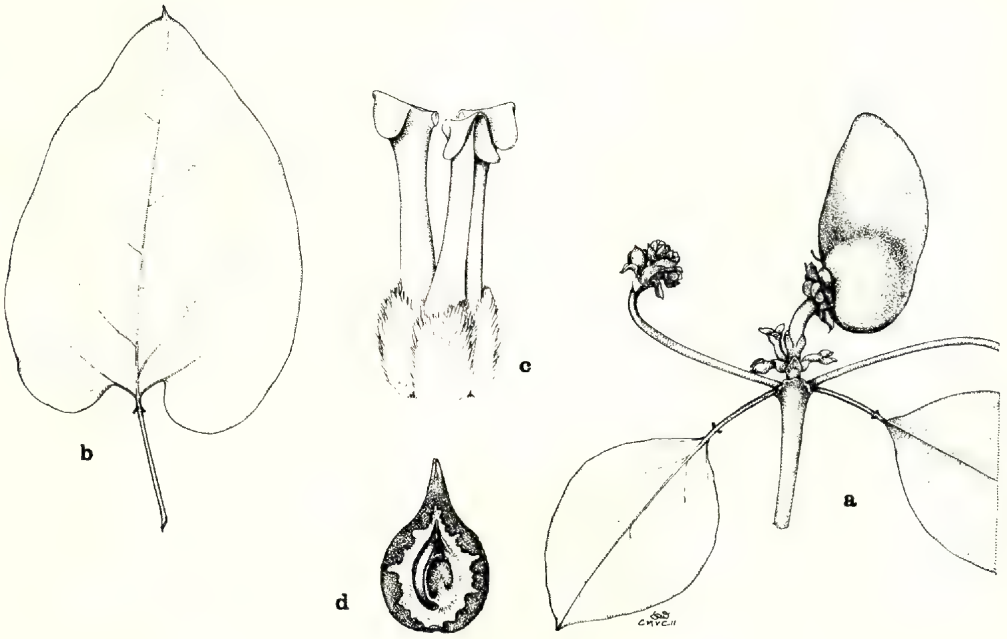

FIG. 5. *Stigmaphyllon jobertii.* a. Portion of inflorescence bearing one samara (×1). b. Leaf (×0.5). c. Gynoecium (×7.5); anterior style in center. d. Longitudinal section through nut to show locule embedded in spongy tissue (×1). (Based on *Jobert 1114.*)

peduncles 2–2.5 mm long; pedicels 5.6–6.5 mm long; peduncles ca. 0.4 times as long as the pedicels; bracts 1.8–2.3 mm long, 1.8–2 mm wide; bracteoles 1.5–1.7 mm long and wide. Sepals ca. 2.5 mm long, 2.5–3 mm wide, glands 1.8–2 mm long, ca. 1 mm wide. Petals not seen. Stamens unequal in size, those opposite the anterior-lateral sepals and posterior-lateral petals with the longest filaments, anthers of those opposite the lateral sepals not seen, other anthers all glabrous. Anterior style ca. 2.6 mm long, shorter than the posterior two, glabrous, erect; apex ca. 1.3 mm long, each foliole ca. 1.2 mm long, ca. 0.8 mm wide, triangular. Posterior styles ca. 3 mm long, glabrous, slightly lyrate; each foliole ca. 1.3 mm long, ca. 0.6 mm wide, parabolic. Dorsal wing of samara encircling the nut, 2.6 cm high measured from base of nut, 1.4 cm wide; nut ca. 13 mm high, ca. 10 mm in diameter, smooth, locule embedded in spongy tissue, areole ca. 3.5 mm long, ca. 4 mm wide, concave, carpophore up to 5 mm long. Embryo not seen.

This distinctive species is known only from one incomplete specimen. It is easily recognized by its distinctive petiole glands and samaras. The cordate laminas are nearly glabrous, and the basal glands are peg-shaped and borne on the petiole, often obliquely, up to 3 mm below the lamina. In South America, such glands are found only in the Colombian *S. romeroi* Cuatrec.; they are also present in *S. sagraeanum* Adr. Juss. and *S. microphyllum* Griseb., and occasionally in *S. emarginatum* (Cav.) Adr. Juss., all of the West Indies. The flowers are borne on very short peduncles and pedicels, and are aggregated into umbellate clusters. The samara, similar to that of *S. adenodon* var. *adenodon* and *S. lacunosum* Adr. Juss., has the reduced dorsal wing surrounding the enlarged nut but lacks lateral winglets. In *S. adenodon* and *S. lacunosum,* as well as several other species, the nut is so large because the locule is surrounded by the air chambers, presumably an adaptation for dispersal by water; typically, the embryo is much larger than

that of species in which the samara is wind-dispersed. *Stigmaphyllon jobertii* differs in that the locule is surrounded by a thick layer of spongy tissue. The type includes two samaras, but in each the embryo was destroyed by insects.

The species is named for Clemens Jobert, who collected the type while accompanying C. A. W. Schwacke on an expedition to the Amazon Basin (Urban 1906).

Stigmaphyllon stenophyllum C. Anderson, sp. nov.—TYPE: COLOMBIA. Antioquia: Mpio. Medellín, Correg. Sta. Elena, Km 1 sobre la via Medellín-Ríonegro, 2000 m, 20 July 1986, *Callejas 2151* (holotype: MICH!; isotype: NY!).

Fig. 6.

Liana. Laminae 9–11.5 cm longae, 1.7–3 cm latae, anguste lanceolatae, supra glabrae, subtus pilos T-formes sparsos ferentes, margine eglanduloso. Inflorescentia solitaria vel dichasialis constata ex umbellis (pseudoracemis congestis?), floribus in quoque pseudoracemo ca. 15–20. Pedunculi 0.8–3 mm longi; pedicelli 10–15 mm longi. Petala margine digitiforme glanduloso-fimbriato; petala lateralia limbo orbiculari; petalum posticum limbo late elliptico. Stamina subaequalia, antheris glabris. Stylus anticus ca. 2.7 mm longus, apice ca. 0.8 mm longo, ca. 0.2 mm lato, lineari; styli postici ca. 2.7 mm longi, lyrati, apice ca. 0.9 mm longo, ca. 0.3 mm lato, lineari. Samara ignota.

Vine. Laminas 9–11.5 cm long, 1.7–3 cm wide, narrowly lanceolate, apex mucronate, base cordate, glabrous above, sparsely pubescent with T-shaped hairs below but densely so along the margins and on the midrib, margin eglandular, with a pair of prominent but sessile glands at apex of the petiole, each gland 0.6–0.7 mm in diameter; petioles 2–2.8 cm long; stipules ca. 0.5 mm long. Flowers ca. 15–20 per umbel (condensed pseudoracemes?), these borne solitary or in dichasia; peduncles 0.8–3 mm long; pedicels 10–15 mm long; peduncles 0.1–0.2 times as long as the pedicels; bracts 1.2–1.5 mm long, ca. 1 mm wide, triangular; bracteoles 1.5–1.7 mm long, 0.7–1 mm wide, narrowly triangular. Sepals ca. 2.5 mm long and wide, glands ca. 2 mm long, ca. 1 mm wide. All petals with the limbs glabrous, suffused with red, margin digitately glandular-fimbriate, the fimbriae up to 0.5 mm long; lateral petals with the limbs orbicular; anterior-lateral petals: claw ca. 3 mm long, limb ca. 8 mm long and wide; posterior-lateral petals: claw ca. 2.5 mm long, limb ca. 6.5 mm long and wide; posterior petal: claw ca. 3.2 mm long, apex very slightly indented, limb ca. 5 mm long and wide, broadly elliptical. Stamens equal in shape, unequal in size; anthers glabrous. Anterior style ca. 2.7 mm long, subequal to the posterior two, with scattered hairs in the proximal 1/2; apex ca. 0.8 mm long including a spur ca. 0.2 mm long, ca. 0.2 mm wide, linear, folioles absent. Posterior styles ca. 2.7 mm long, with scattered hairs in the proximal 1/2, erect; apex ca. 0.9 mm long including a spur ca. 0.2 mm long, ca. 0.3 mm wide, linear, slightly incurved, folioles absent. Samara not seen.

Stigmaphyllon stenophyllum is known only from the type collection. It is readily recognized by its short-petioled, narrowly lanceolate leaves up to 3 cm wide, which are sparsely beset with T-shaped hairs below though densely so on the midrib and margin. The peduncles are very short (0.8–3 mm) and only 0.1–0.2 times as long as the pedicels. In other respects, this species most closely resembles the sympatric *S. bogotense* Tr. & Pl., which differs in its long-petiolate leaves with elliptical to ovate to suborbicular laminas abundantly pubescent below, and longer peduncles and pedicels [peduncles 0.3–0.8 (–1) times as long as the pedicels]. In

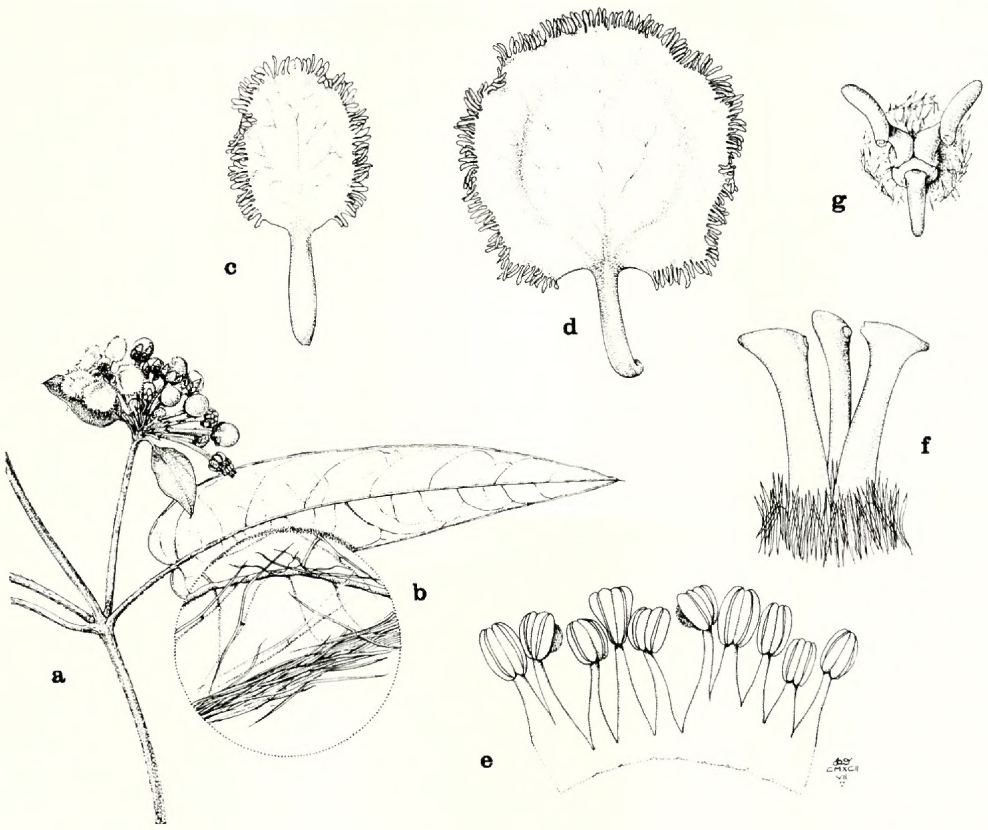

FIG. 6. *Stigmaphyllon stenophyllum.* a. Flowering branch (×0.5). b. Detail of abaxial leaf surface (×15). c. Posterior petal (×4). d. Anterior-lateral petal (×4). e. Androecium (×5); second stamen from right opposing posterior petal. f. Gynoecium (×10); anterior style at right. g. Gynoecium seen from above (×10); anterior style at bottom. (Based on *Callejas 2151.*)

both species, the flowers are arranged in umbels and condensed pseudoracemes, in which the basal two are separated a short distance from the cluster, the androecium is homogeneous—none of the anthers have enlarged connectives and reduced locules, and the styles are efoliolate.

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